Structure et connectivité de la mégafaune marine à l'échelle d'une région océanique : enjeux pour la gestion durable des tortues vertes dans l'océan Indien occidental

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THESE

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Par : **Jérôme BOURJEA**

Structure et connectivité de la mégafaune marine à l'échelle d'une région océanique

Enjeux pour la gestion durable des tortues vertes dans l'océan Indien occidental

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STRUCTURE ET CONNECTIVITE DE LA MEGAFAUNE MARINE A L'ECHELLE D'UNE REGION OCEANIQUE : ENJEUX POUR LA GESTION DURABLE DES TORTUES MARINES DANS L'OCEAN INDIEN OCCIDENTAL

Résumé

Ce travail de thèse s'insère dans une démarche globale d'acquisition des connaissances sur la tortue verte (*Chelonia mydas*) dans l'océan Indien occidental et ce afin de disposer d'éléments scientifiques essentiels à la mise en place d'une gestion cohérente et efficace de cette espèce menacée.

Dans un premier temps, appliquant différentes modèles statistiques, ce travail a visé à établir des données de référence sur l'abondance des tortues vertes femelles en reproduction et les tendances sur le long terme des principales populations. Dans un second temps, il a consisté à déterminer la structure génétique et les relations qui existent entre les différentes populations de cette espèce. Enfin, la conservation des tortues marines étant étroitement liée aux pressions extérieures, ce travail a tenté dans un troisième temps de caractériser les pressions anthropiques qu'elles subissent, et notamment celles liées à la pêche.

L'ensemble de ces résultats a permis de réaliser des avancées majeures dans la connaissance de la biologie et de l'écologie de la tortue verte et de disposer d'une vision régionale fiable de l'état de conservation de cette espèce dans l'océan Indien occidental. Leur compilation a ainsi permis d'identifier des zones régionales prioritaires de protection mais aussi des sites de vigilance plus spécifiques comme celui d'Europa. Enfin cette synthèse met en lumière les priorités de recherche et les approches scientifiques à favoriser à l'avenir pour améliorer les connaissances et affiner les priorités de conservation non seulement des tortues marines, mais aussi de la mégafaune marine en général.

Mots clés

tortues marines ; tortue verte ; *Chelonia mydas* ; mégafaune ; évaluation de population ; tendance sur long terme ; structure génétique ; génétique des populations ; capture accidentelle ; biologie de la conservation ; unité de gestion ; océan Indien

POPULATION STRUCTURE AND CONNECTIVITY OF MEGAFAUNA AT THE OCEANIC REGION SCALE: KEYS ISSUES FOR SUSTAINABLE MANAGEMENT OF MARINE TURTLES IN THE INDIAN OCEAN

Abstract

This thesis is a comprehensive work aiming to improve scientific knowledge on the green turtle (*Chelonia mydas*) in order to provide key scientific evidences needed for the implementation of coherent and effective management measures to protect at the Western Indian Ocean scale this threatened species.

In a first step, this work aimed to established baseline data on the abundance of green turtles nesting females and long term trends of some key nesting populations of the region by applying different modelling methods. In a second step, this work determined the regional genetic structure of this species and the relationships that exists between the different populations. Finally, the conservation of marine turtles being closely dependant to external pressures, this work tried to characterize the anthropogenic pressures they face, more specifically those related to fishing activities.

All these results allowed unraveling some key gaps on the biology and ecology of the green turtle in the region and led to a global vision of the conservation status of this species in the Western Indian Ocean. The compilation of the results enabled the identification of regional priority areas for protection, but also some more specific threatened sites such as Europa. Finally, this synthesis sheds light on research priorities and scientific approaches to be promote in the future to unlock other key scientific issues and refine conservation priorities, not only of marine turtles, but also of marine megafauna as a whole.

Key words

Marines turtles ; green turtle ; *Chelonia mydas* ; megafauna ; population assessment ; long term trend ; genetic structure ; population genetic ; by-catch ; incidental catch ; biological conservation ; management units ; Indian ocean

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J'espère que ce document vous plaira et que son contenu apportera sa pierre à l'édifice car, comme le disait Baudelaire, « qu'importe le flacon pourvu qu'on ait l'ivresse… »

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SIGLES

AMP (MPA): Aire Marine Protégée / Marine Protected Area

BED : By-catch Excluding Devices / Système d'exclusion des captures accidentelles

CDB : Convention sur la Diversité Biologique

CITES : Convention on the International Trade of Endangered Species / Convention sur le commerce international des espèces de faune et de flore menacées d'extinction

CMS : Convention on Migratory Species / Convention sur les espèces migratrices

CSE : Courant Sud Equatorial

CTOI (IOTC): Commission des Thons de l'Océan Indien / Indian Ocean Tuna Commission

DCP : Dispositif de Concentration de Poisson

ERA : Ecological Risk Assessment / Evaluation des risques écologiques

EvoIA : Evolutionary Impact Assessments / Evaluation de l'impact sur l'évolution

FST : Front hydrochimique Sud Tropical

GADM : Global Administrative Areas database – http://www.gadm.org/

GeM : Genetic monitoring / échantillonnage génétique

IOSEA MoU : Mémorandum d'accord sur la conservation et la gestion des tortues marines et de leur habitat de l'océan Indien et de l'Asie du Sud-Est

ISSG: Indian South Subtropical Gyre Province / Province du gyre subtropical sud de l'océan Indien

MONS: Indian Monsoon Gyre Province / Province du gyre de la mousson indienne

NMC : Nord du canal du Mozambique (unité génétique du)

PNA (NAP) : Plan National d'Actions / National Action Plan

PSA : Productivity and Susceptibility Analysis / Analyses de production et sensibilité

RBA : Rapid Bycatch Assesment / Evaluation rapide des captures accidentelles

SEY : Seychelles (unité génétique des)

SMC : Sud du Canal du Mozambique (unité génétique du)

SNP : Single Nucleotide Polymorphism / Polymorphisme d'un seul nucléotide

SWIOFP : South West Indian Ocean Fishery Project / Projet sur la pêche du sud-ouest de l'océan Indien

TED : Turtle Excluding Device / Système d'exclusion de tortues

UICN : Union Internationale pour la Conservation de la Nature

RMU (UGR) : Régional Management Unit / Unité de gestion régionale

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PREAMBULE

Le contexte de cette thèse a été particulier. En effet, sa rédaction ne s'est pas déroulée de manière standard, c'est à dire initiée à la suite des études et finalisée en trois ou quatre ans, l'auteur étant à 100% engagé dans son sujet de thèse.

Cadre de recherche permanent à l'Ifremer en tant qu'ingénieur en halieutique de l'Ecole Normale Supérieure d'Agronomie de Rennes, j'ai passé les dix dernière années à faire de la recherche appliquée dans le domaine de la biologie des pêches (modèles biologiques utilisés : l'espadon *Xiphias gladius* et le thon germon *Thunnus alalunga*) et de la conservation (tortues marines et concept d'aires marines protégées). En concertation avec l'Ifremer et mon comité de suivi de thèse, il a été décidé de réaliser une thèse sur publications. Celle-ci ne devait pas reprendre l'ensemble de mes travaux scientifiques mais cibler un modèle biologique et une problématique.

Ainsi, le choix du sujet s'est porté sur le modèle biologique « tortue verte » et la problématique de la conservation de la mégafaune migratrice à l'échelle régionale. En exploitant six publications rédigées entre 2007 et 2014, la rédaction de cette thèse a donc été structurée autour de ces publications en les complétant par une introduction, des synthèses de chapitres abordant une problématique particulière (l'évaluation des populations, la structure génétique et les interactions avec la pêche) et une conclusion générale proposant non seulement une synthèse globale de ces travaux mais aussi une ouverture plus générale sur la gestion de la mégafaune dans l'océan Indien.

Cette rédaction s'est déroulée en parallèle avec mon travail à l'Ifremer, mais aussi avec la gestion de quatre projets dont j'étais le porteur, sans oublier les différentes expertises dont je suis responsable.

INTRODUCTION

La biologie de la conservation, une discipline de crise dans un monde en crise.

La croissance de la population humaine et le développement des technologies qui en découle, ont été exponentiels ces derniers siècles (Myers et Simons, 1994), si bien qu'on ne peut être optimiste quant à l'avenir de la biodiversité de la planète (Pimm et al., 1995). Pour le moins, en ce qui concerne la biodiversité, cette évolution sociétale a eu le rare avantage de nous faire comprendre l'importance qu'avaient pour l'humanité les espèces animales et végétales qui constituent notre patrimoine naturel (Ehrlich et Ehrlich, 1981). En effet, le taux d'extinction des espèces a subi une croissance considérable au fil de ces derniers siècles. Elle est aujourd'hui estimée comme étant 1 000 fois supérieure à celle d'avant l'apparition de l'Homme (Pimm et al., 2014). Cette érosion de la biodiversité s'associe à une dégradation générale des écosystèmes et des services écosystémiques associés. Ce constat irréfutable, auquel s'ajoutent des financements malheureusement trop restreints, implique la nécessité de prioriser les actions de conservation de cette biodiversité (Brooks et al., 2006) et la mise en place urgente de modèles prédictifs de sa dégradation adaptés à leur utilisation par les gestionnaires (Sutherland et Freckleton, 2012).

C'est pour répondre à cette crise d'extinction des espèces dont les hommes sont responsables que la biologie de la conservation a émergé vers la fin des années 1960 sous la forme d'une nouvelle discipline hybride. Celle-ci s'est développée à partir de la fin des années 70 (Soulé 1980) avec comme axes principaux (i) d'étudier, comprendre et estimer l'impact des activités anthropiques sur les espèces et les écosystèmes et (ii) de développer des solutions rapides et pratiques pour prévenir l'extinction des espèces les plus menacées. Holt et Talbot (1978) ont été les premiers à proposer une série de principes à la fois théoriques et pratiques, pour assurer la conservation des ressources vivantes sauvages, principes repris et complétés par Mangel et al. (1996). L'ambition de ces principes est d'associer science et gestion pour le maintien de la diversité du vivant sur la planète (Soulé 1986). La biologie de la conservation est donc une discipline de crise qui applique les principes de l'écologie, de la biogéographie, de la génétique des populations, de l'anthropologie, de l'économie, de la sociologie, etc., au maintien de la diversité biologique sur l'ensemble de la planète. Par les objectifs qu'elle s'est fixée au départ (la protection d'une espèce observée comme gravement menacée), c'est une science de l'action qui doit agir souvent avant de connaître les faits, et qui repose principalement sur l'analyse des processus de maintien de la biodiversité à différents niveaux spatio-temporels, et avec pour but de fournir des éléments tangibles pour la gestion conservatoire et durable des espèces et des milieux. Elle doit passer du statut de science qui enregistre des catastrophes à celui d'une science d'action, qui permette d'élaborer des plans de gestion scientifiquement fondés pour empêcher les catastrophes écologiques.

La protection d'une espèce pour la protection de l'écosystème

La biologie de la conservation s'est concentrée dès le départ sur la notion d'espèce dans une optique de sauvegarde. L'espèce est un concept central dans cette discipline car c'est à la fois une entité taxonomique qui présente un réel sens évolutif et une unité pratique accessible et visible. En effet, la plupart des activités de conservation sont centrées sur l'espèce comme unité de mesure de la biodiversité plus pratique que l'écosystème ou les gènes. Par exemple, l'Union Internationale pour la conservation de la Nature (UICN) se base sur la notion d'espèce pour établir les critères de la liste rouge des espèces menacées de la planète (IUCN, 2012), qui est exploitée pour quantifier leurs risques d'extinction (Mace et al., 2008). Cette notion de risque est centrale car elle sert de levier à de nombreux pays pour la mise en place de mesures de conservation concrètes et ciblées. Partout dans le monde, l'espèce demeure donc l'outil préférentiel de la conservation car c'est avant tout une unité légale, facilement identifiable et bien plus évocatrice pour le grand public.

Si de nombreuses définitions ont été données pour une espèce en fonction de l'angle scientifique abordé (Fraser et Bernatchez, 2001), cette notion implique celle de population associée. C'est dans les années 1970-1980 que l'écologie a développé le paradigme de 'la biologie des populations' chez les plantes (Harper, 1977), les populations étant considérées aujourd'hui comme des unités biologiques fondamentales et fonctionnelles, pouvant être définies comme des groupes d'individus de même espèce, interféconds et montrant une disjonction spatiale, génétique et/ou démographique les uns avec les autres. Car agir pour la conservation d'une espèce passe avant tout par l'assurance du maintien du bon état de santé de ses populations. Les sources de financement et les moyens alloués étant limités, avant d'agir à l'échelle de la population, il faut identifier les espèces prioritaires à protéger. Les concepts d'espèce 'clef de voûte'[1], d'espèce 'parapluie'[2], d'espèce 'porte-drapeau'[3] – ou emblématique (Simberloff, 1998; Barrua, 2011) ou encore d'espèce 'peluche' (Ballouard et al., 2011) sont autant de dénominations possibles qui justifient d'autant plus la conservation d'une unique espèce qu'elle en favorise de multiples autres à l'échelle d'un type d'habitat, d'une communauté ou d'un écosystème. Par exemple, les grands mammifères carnivores à large distribution ont souvent servi à protéger de larges zones géographiques (voir synthèse dans Roberge et Angelstam, 2004) pour le plus grand bénéfice des autres espèces.

En effet, si la conservation se justifie par le choix d'une espèce, le constat établi au début du XXI^{ème} siècle montre que 20 à 70% des surfaces de 11 des 13 biomes de la planète ont été atteints et modifiés par l'homme (Millennium Ecosystem Assessment, 2005). A l'image de l'UICN travaillant à la mise en place de qualification de l'état de santé des écosystèmes (Rodriguez et al., 2008), la biologie de la conservation tend donc au XXIème siècle vers une approche écosystémique.

[1] Espèce qui a un effet disproportionné sur son environnement comparativement à ses effectifs ou à sa biomasse

[2] Espèce dont l'étendue du territoire permet la protection d'un grand nombre d'autres espèces si celle-ci est protégée

[3] Espèce emblématique mise en valeur afin de faire augmenter le soutien offert à la conservation de la biodiversité

Les challenges de la biologie de la conservation au XXIème siècle

Les challenges de la biologie de la conservation en ce début de XXI^{ème} siècle sont donc ambitieux. Outre le fait que cette discipline tend vers une approche « écosystème », et qu'elle tente d'optimiser ses recommandations pour préserver un maximum d'espèces et d'habitats associés, il n'en reste pas moins que parfois dans une situation de crise naturelle, il faut agir. Et cette action doit souvent se mettre en place avant même de connaître tous les faits, sans pouvoir faire d'expérimentations ou de répliquas et sans avoir aucun recul sur les conséquences potentielles d'une mesure de conservation sur d'autres compartiments/espèces de l'écosystème. La conservation d'une espèce, d'un habitat, tient donc aujourd'hui en notre capacité à anticiper ces phases de crise et à éviter l'irréversibilité de l'impact anthropique sur les écosystèmes, tout en s'adossant à quatre principes fondamentaux : le principe de précaution[4], d'humanité[5], de réversibilité[6] et de gestion adaptative[7]. Et pour être capable d'anticiper ces crises, la biologie de la conservation doit se focaliser sur trois piliers de base indispensables à la réalisation d'avis scientifiques pertinents et fondés destinés aux gestionnaires.

Le premier pilier consiste à évaluer l'abondance de l'espèce dans ses différentes classes d'âge et d'estimer la tendance sur le long terme de l'abondance de l'ensemble des populations. Ce pilier nécessite donc une excellente connaissance de la biologie et de l'écologie de l'espèce, de ses traits de vie et de leur évolution dans le temps (Pearson et al., 2014). Mais compte tenu de la complexité de ces paramètres pour la majorité des espèces, et notamment celles des grands migrateurs, ainsi que des coûts associés à un suivi sur le long terme de ces paramètres, elle implique aussi notre capacité à trouver/développer des indicateurs fiables reflétant cette évolution. Agissant sur la notion de population, ce pilier induit irrémédiablement la nécessité de mieux comprendre la structure spatiale des populations et les liens qui existent avec les populations adjacentes.

Le second pilier est la connaissance de la structure spatiale des populations, liée au domaine vital de l'espèce, sa dynamique spatiale et sa capacité à se disperser à tous les stades de vie. Un des moyens les plus efficaces pour répondre à ces questions, et notamment dans une vision sur le long terme, est la génétique des populations. Appliquée à la conservation, cette discipline est appelée la génétique de la conservation. Cette discipline est une science appliquée exploitant la diversité génétique et l'évolution moléculaire pour évaluer l'état de «santé génétique» des populations, la structure spatiale et la connectivité/flux de gènes entre populations. En d'autres termes, cette approche permet d'évaluer l'état de conservation génétique de la population d'une espèce ainsi que ses relations avec d'autres populations de la même espèce ou d'espèces proches (Allendorf et Luikart, 2006; Frankham et al., 2010; Frankham, 2010). Par exemple, le calcul de la diversité phylogénétique, inter ou intra espèce, montre que la protection d'une

[4] Mise en place des mesures pour prévenir des risques, lorsque la science et les connaissances techniques ne sont pas à même de fournir des certitudes

[5] Qui doit prendre en compte le respect de l'ensemble des Hommes

[6] Toute action entreprise doit pouvoir permettre un retour à son état initial si elle ne fonction pas

[7] Processus systématique d'amélioration constante des politiques et pratiques de gestion qui se base sur les leçons tirées des résultats de politiques et pratiques antérieures

population aux frontières de son domaine vital augmente significativement la conservation de sa diversité génétique (Faith, 1992).

Enfin le troisième pilier est la connaissance des menaces qui pèsent sur ces espèces. Il faut donc les qualifier, les quantifier et les hiérarchiser afin d'être capable de donner des priorités aux actions de protection à mettre en place. Par exemple, il est maintenant reconnu que les deux principales menaces qui pèsent sur la biodiversité marine sont les interactions liées aux activités humaines, et notamment la pêche (Lewinson et al., 2014) et les changements globaux (e.g. le changement climatique ; Pearson et al., 2014).

Les conventions internationales, fondation de la conservation des espèces migratrices

Du fait des menaces qui pèsent sur ces espèces et en particulier sur les espèces migratrices transfrontalières sur lesquelles une action internationale est indispensable, de nombreuses conventions et outils internationaux se sont mis en place depuis les années 70 afin de favoriser la préservation de ces espèces. Ils servent avant tout de support à la biologie de la conservation en légiférant en droit international ou national sur le statut des espèces menacées. Ils servent également à prioriser indirectement de grandes lignes d'actions à mettre en place nécessaires à la canalisation des financements. On trouve entre autres :

- **Convention RAMSAR** sur la conservation des zones humides, signée en 1971 et ratifiée par la France en 1986. La convention RAMSAR protège les zones humides d'intérêt mondial qui présentent des caractéristiques écologiques exceptionnelles. On retrouve dans l'océan Indien des sites RAMSAR à Mayotte et à Europa.

- **Convention de Washington** ou Convention sur le commerce international des espèces de faune et de flore menacées d'extinction – CITES, signée en 1973 et ratifiée par la France en 1978. Cette convention internationale a pour but de réguler le commerce international des espèces menacées. Les espèces bénéficient de différents degrés de protection en fonction de leur surexploitation (Annexes I, II et III).

- **Convention de Bonn** ou Convention sur les espèces migratrices – CMS, signée en 1979 et ratifiée par la France en 1990. Cette convention internationale vise à protéger les espèces migratrices terrestres et aquatiques sur l'ensemble de leurs aires de répartition.

- **Convention de Berne** ou Convention relative à la conservation de la vie sauvage et du milieu naturel de l'Europe, signée en 1979 et ratifiée par la France en 1990. Cette convention européenne se focalise sur la protection de la faune et la flore sauvages et concerne principalement l'Europe continentale. Cependant on y retrouve par exemple des espèces emblématiques comme les tortues marines en Annexe II. Si les régions

ultrapériphériques françaises sont inclues dans cette convention, il n'en est pas de même des îles Eparses.

- **Convention de Rio** ou convention sur la diversité biologique – CDB, signée en 1992 et ratifiée par la France en 1994. Cette convention reste floue sur son application au milieu marin et notamment les eaux internationales. Cependant cette convention très généraliste sur la biodiversité, vise à préserver la diversité biologique, à tendre vers une utilisation durable des éléments naturels et à aboutir à un partage équitable des ressources naturelles.

A ces conventions internationales, s'ajoutent également des conventions régionales qui peuvent être déterminantes au niveau spécifique. Dans le cas de l'océan Indien et des tortues marines par exemple, elles sont très actives et dynamisent depuis un certain nombre d'années les actions de conservation de ces espèces dans cet océan :

- **Convention de Nairobi** ou Convention pour la protection, la gestion et la mise en valeur du milieu marin et côtier de la région de l'océan Indien occidental, signée en 1985 et ratifiée par la France en 1989. Cette convention a pour objectif d'assurer la protection et la gestion du milieu marin et des zones côtières dans la zone d'application de la convention, de prévenir, de réduire et de combattre la pollution de cette zone et d'assurer une gestion des ressources naturelles qui soit rationnelle du point de vue de l'environnement.

- **Mémorandum d'accord sur la conservation et la gestion des tortues marines et de leur habitat de l'océan Indien et de l'Asie du Sud-Est** – IOSEA MoU, signé en 2001 et ratifié par la France en 2010. Ce MoU, sous l'égide de la CMS, a pour objectif de protéger et préserver les tortues et leur habitat dans l'océan Indien et le sud-est asiatique. Même s'il n'est pas contraignant juridiquement, il reste très influent pour la protection de ces espèces dans cette région du monde.

- **Résolution CTOI 12/04** concernant les tortues marines dans le Recueil des Mesures de conservation et de gestion actives de la Commission des Thons de l'Océan Indien – CTOI. Cette résolution s'appliquant à tous les pays signataires de la CTOI et concerne les bonnes pratiques à adopter pour atténuer l'impact de la pêche hauturière sur les tortues marines.

Enfin, plus spécifiquement pour la conservation des espèces menacées, l'outil de conservation actuellement le plus influent est la classification de la **Liste Rouge de l'UICN** (IUCN, 2012). Elaborée par des centaines d'experts de par le monde, cette liste constitue l'inventaire le plus complet de l'état de conservation des espèces animales et végétales de la planète. Elle fournit pour chaque espèce, une série d'indicateurs de l'état de santé de la population (taille des populations, distribution, effectif minimum de reproduction, tendance sur le long terme...).

Tableau 0.1 : Statuts de protection internationaux des tortues marines (sources et pour plus de détails sur les annexes, voir Philippe et al. soumis)

Textes	Espèces	*Chelonia mydas*	*Eretmochelys imbricata*	*Caretta caretta*	*Dermochelys coriacea*	*Lepidochelys olivacea*
	Nom commun	*Tortue verte*	*Imbriquée*	*Caouanne*	*Luth*	*Olivâtre*
Conventions internationales	**Washington, 1972** *CITES (commerce international des espèces)*	annexe I	annexe I	annexe I	annexe I	annexe I
	Bonn, 1979 *CMPS (Convention on Migratory Species)*	annexes I et II	annexes I et II	annexe I	annexe I	annexe I
	Berne, 1979 *Conservation de la vie sauvage*	annexe II	annexe II	annexe II	annexe II	annexe II
	Rio, juin 1992 *Conservation de la diversité biologique*	Ce texte vise à protéger la diversité biologique en général				
Conventions régionales	**IOSEA Mémorandum d'accord (annexé à la convention CMS)**	Protéger, conserver et reconstituer les populations de tortues marines et leurs habitats dans l'océan Indien : signature de la France le 05 décembre 2008				
	Nairobi, 1985 *Protection et gestion du milieu marin de l'océan Indien Occidental*	annexes III et IV	annexes III et IV	annexes II et IV	annexes I I et IV	annexes II et IV
Inventaire mondial	**Liste Rouge UICN**	danger d'extinction	danger critique d'extinction	danger d'extinction	danger critique d'extinction	vulnérable

Le tableau 0.1 donne l'exemple de l'application de ces conventions et outils internationaux aux tortues marines.

L'océan Indien occidental, « point chaud » de biodiversité

Ne pouvant préserver l'ensemble des espèces et des écosystèmes de la planète pour des considérations économiques évidentes, la gestion de la biodiversité nécessite la mise en place d'un compromis entre coût de la conservation et protection effective des espèces et de leur écosystème. Myers (1988; 1990) a développé le concept de «point chaud» de la biodiversité, c'est-à-dire des zones présentant une concentration exceptionnelle d'espèces endémiques et subissant des pertes d'habitats écologiques importantes. Nous utiliserons par la suite le terme anglophone de « Hotspot ». Dans cette approche, le sud-ouest de l'océan Indien (i.e dans ce cas Madagascar et les îles de la région) a été considéré comme le hotspot le plus important de la planète sur les 25 identifiés (Myers et al., 2000), et identifié comme une priorité de gestion de la biodiversité. Plus récemment, l'Unesco a précisé sur la base d'une étude regroupant de nombreux experts de la région, que 10 sites potentiels devaient faire partie du patrimoine mondial marin de l'humanité (Obura et al., 2012). Ces conclusions ont été notamment établies sur la base du caractère exceptionnel des écosystèmes coralliens (Obura, 2012), de mangrove

(Alongi, 2002; Wilkie et Fortuna, 2003), d'herbiers de phanérogames (Gullström et al., 2002; Duarte et al., 2008) et de la biodiversité que l'on y trouve.

A l'image de la colonisation des mammifères terrestres de Madagascar grâce aux courants océaniques dans lesquels a baigné cette île-continent durant le paléogène (période succédant à l'extinction de la fin Crétacé; Ali and Huber, 2010), la courantologie contemporaine a joué et joue très certainement un rôle majeur dans les processus d'isolement et de connectivité entre différentes populations d'une même espèce dans cette région. L'effet des courants dans la dispersion des nouveau-nés de tortues marines par exemple a déjà clairement été démontré dans les océans Pacifique (tortue luth; Gaspar et al., 2012), Atlantique (tortue imbriquée; Putman et al., 2014) et en Méditerranée (tortue caouanne; Casale et Mariani, 2014).

L'océan Indien est dominé dans l'hémisphère sud par le Courant Sud Equatorial – CSE s'écoulant d'est en ouest (Schott et al., 2009). Il est aussi caractérisé autour de 12°S par le Front hydrochimique Sud Tropical – FST qui sépare deux grandes provinces océaniques oligotrophes, celle du gyre de la mousson indienne (Indian Monsoon Gyre Province – MONS) au nord, celle du gyre indien subtropical (Indian South Subtropical Gyre Province – ISSG) (Longhurst, 1998). Au sein de la zone du sud-ouest de l'océan Indien, plusieurs auteurs ont mis en évidence le caractère très particulier et complexe des courants océaniques (voir synthèse dans Schott et al. 2009). Ces auteurs ont entre autre montré que le flux dominant du canal du Mozambique était sous le contrôle de tourbillons méso-échelles agissant comme des mécanismes perturbant les phénomènes de connectivité (Schouten et al., 2003, Swart et al., 2010). En effet, le CSE se scinde en deux au niveau de Madagascar, aux alentours de la latitude 17°S, formant au nord le courant côtier Est Africain s'écoulant vers le nord (autour de 10°S) et créant vers le sud une succession de tourbillons méso-échelle avant de rejoindre le Courant des Aiguilles (voir Fig.0.1 pour une représentation complète du système courantologique en fonction des périodes de mousson).

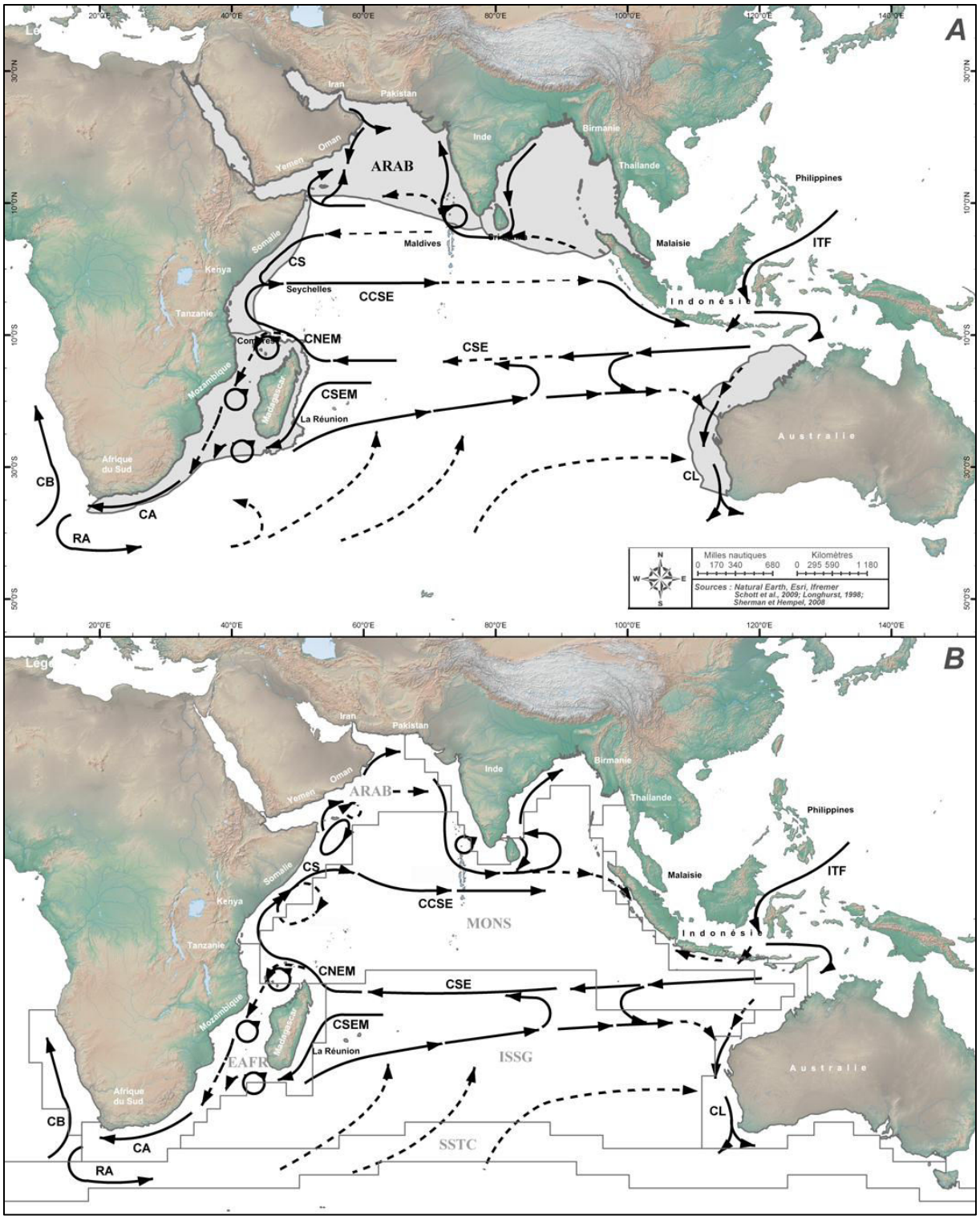

Fig.0.1 : Principaux courants de l'océan Indien, provinces écologiques de Longhurst (1998) et grands écosystèmes marins (zone grisée; d'après Sherman et Hempel, 2008). A: période de Mousson de nord-est (hiver boréal); B : période de Mousson de sud-ouest (été boréal). Les lignes indiquent les provinces biogéographiques de Longhurst et les noms associés en caractères réguliers : MONS : Indian Monsoon Gyre Province; ISSG: Indian South Subtropical Gyre Province; ARAB : Arabian Sea Upwelling Province ; SSTC : Province de la convergence sud subtropicale ; EAFR : province de la côte est africaine. Principaux courants : CSE : courant sud Equatorial; CCSE : Contre-Courant Sud Equatorial; CNEM : Courant Nord Est Malgache; CSEM : Courant Sud Est Malgache; CS : Courant côtier est africain; CA : Courant des Aiguilles; RA : Rétroflexion des Aiguilles; CB : Courant du Bengale; ITF : Courant Indonésien ; LC : Courant de Leeuwin. Modifié de Schott et al., 2009.

Des études récentes ont montré que ce système hydrodynamique complexe dans le canal du Mozambique, et plus largement dans le sud-ouest de l'océan Indien, pouvait influencer la connectivité des populations d'animaux marins. C'est le cas par exemple de certaines espèces de poissons coralliens comme le poisson perroquet *Scarus ghobban* (Visram et al., 2010), le lutjan à rayures bleues *Lutjanus kasmira* (Muths et al., 2012), le mérou gâteau de cire *Epinephelus mera* (Muths et al., 2014), le cardinal *Myripristis berndti* (Muths et al., 2011) ou des espèces de corail comme *Pocillopora verrucosa* (Ridgway et al., 2001). Obura (2012) a d'ailleurs proposé que les patrons de diversité des coraux dans le sud-ouest de l'océan Indien étaient très certainement liés aux conditions océanographiques de la zone, avec une forte influence du Courant Sud Equatorial transportant des larves depuis l'Asie du sud-est et maintenant la forte diversité observée dans le nord du canal du Mozambique. Cette forte diversité serait à son tour exportée vers les régions environnantes par le jeu des courants (Canal du Mozambique, Mascareignes, Seychelles). Cependant, l'ensemble de ces études montre bien que les patrons de connectivité et les structures de populations qui en découlent, même s'ils sont directement influencés par les courants présents et/ou passés, sont directement dépendants du modèle biologique exploré et des caractéristiques de ces traits de vie.

Le modèle « tortue marine »

Les tortues marines font partie de cette mégafaune emblématique aujourd'hui gravement menacée. Elles sont considérées pour la conservation de la biodiversité comme des espèces «porte drapeau» par l'image qu'elles donnent, et «parapluie» par leur aire de répartition. Elles représentent avec le reste de la mégafaune, de véritables ambassadeurs de la protection de l'environnement. Ces espèces appartiennent aux chordés vertébrés tétrapodes anapsides et amniotes; ce sont des ectotermes et poïkilotermes, de la classe des Sauropsides (dans laquelle on retrouve les oiseaux) et de l'ordre des Testudines (Lecointe et Le Guyader 2002).

Il existe dans le monde sept espèces de tortues marines se regroupant toutes dans la superfamille des Chelonioidea. La tortue verte *Chelonia mydas*, la tortue caouanne *Caretta caretta*, la tortue imbriquée *Eretmochelys imbricata*, la tortue olivâtre *Lepidochelys olivacea*, la tortue de Kemp *Lepidochelys kempii*, la tortue à dos plat *Natator depressus* appartiennent à la famille des Cheloniidae alors que la tortue luth *Dermochelys coriacea*, appartient à la famille des Dermochelyidae. La détermination d'une huitième espèce est actuellement en discussion, la tortue noire *Chelonia agassizii*, proche de la tortue verte (Bowen and Karl 2000). Toutes ces espèces sont considérées comme menacées et donc sur la liste rouge de l'UICN et trois sont en danger critique d'extinction : la tortue luth, la tortue imbriquée et la tortue de Kemp. A ce titre, elles sont prises en compte dans la majorité des conventions internationales (Tableau 0.1). Seules les tortues vertes, imbriquées, olivâtres, caouanne et luth sont présentes dans l'océan Indien occidental. Dans un contexte de conservation exigeant des prises de décision rapides et efficaces, il est indispensable de connaître au mieux le modèle biologique ciblé et sa relation avec l'environnement. Le modèle biologique «tortue marine» est malheureusement complexe. Il regroupe des espèces longévives qui occupent des habitats très différents au cours de leur cycle

biologique. Elles évoluent en mer pour s'alimenter la plupart du temps, mais ont conservé une composante terrestre durant leur cycle biologique lorsque les femelles montent sur les plages pour y déposer leurs œufs.

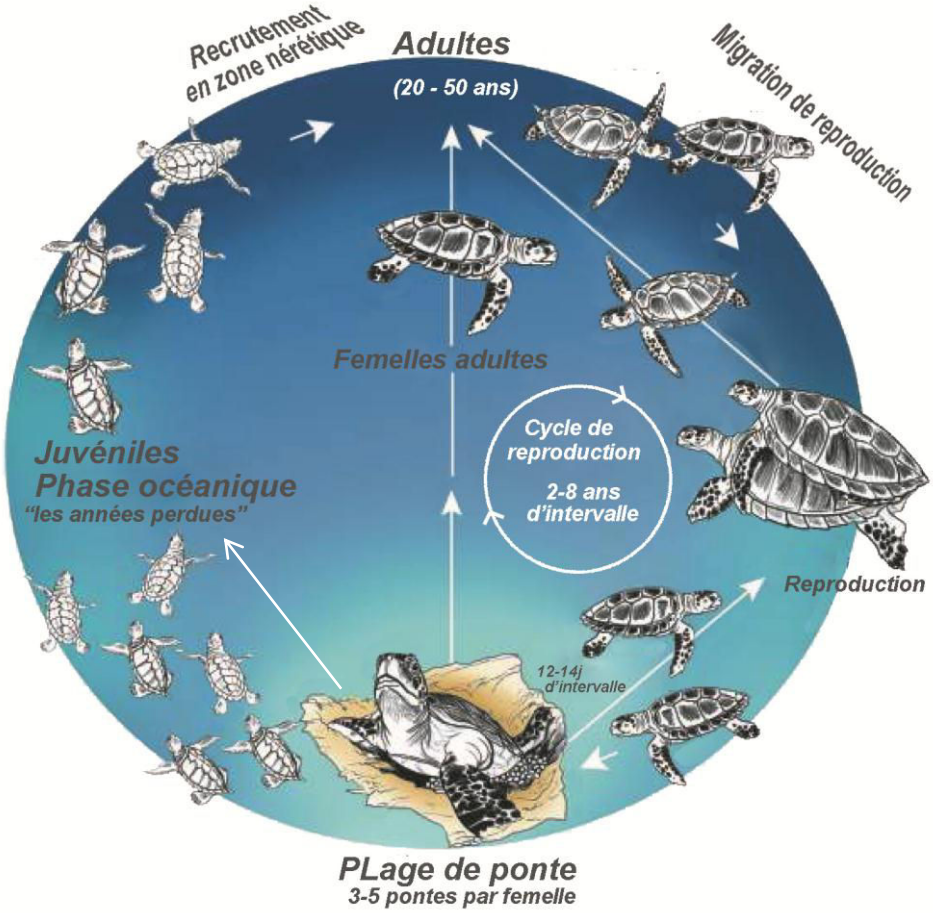

Fig.0.2 : Cycle biologique synthétique des tortues marines (modifié d'après FAO, 2009 et Lanyon et al., 1989)

Le cycle de vie des tortues marines est dans sa globalité relativement bien connu (Fig. 0.2). Il est extrêmement complexe dans l'espace et dans le temps et la télémétrie satellitaire a pu mettre en évidence qu'il intervenait à l'échelle des bassins océaniques aussi bien pour les phases adultes que juvéniles, sur une fenêtre temporelle très large et sur une succession d'habitats différents (terrestre, pélagique, néritique côtier ou hauturier; Godley et al., 2007). Ce cycle étant déjà très bien détaillé dans la littérature (voir synthèse dans Lutz et Musick, 1996; Lutz et al., 2002; Wyneken et al., 2013; et repris dans les chapitres 1, 2 et 3 de ce manuscrit), seuls certains points ayant des implications clés en conservation seront détaillés ici.

Tout d'abord, la complexité de ce modèle biologique réside dans l'espace qu'il occupe. Les adultes de tortues marines sont de grands migrateurs partageant leur temps entre un habitat terrestre, qu'elles fréquentent de manière périodique et saisonnière pour la ponte (e.g. la tortue verte; Dalleau et al., 2012), pélagique lors des migrations de reproduction (e.g. la tortue olivâtre;

Maxwell et al., 2011), et néritique (e.g. la caouanne; McClellan et al., 2010) ou pélagique (e.g. la luth; Fossette et al., 2010) lors de la phase d'alimentation. Les distances entre sites de reproduction et aires d'alimentation peuvent être considérables, dépassant fréquemment plusieurs milliers de kilomètres (voir synthèse dans Luschi et al., 2003). Dans le cas de l'océan Indien par exemple, les tortues vertes migrent en moyenne 1359 ± 832 km (médiane : 1184 km; Max : 4269 km; N = 77), traversent jusqu'à sept zones économiques exclusives différentes avant de rejoindre des habitats d'alimentation répartis dans sept pays différents (Bourjea et al., 2013; Dalleau, 2013). Cette dimension internationale du cycle de vie des adultes rend complexe la gestion des populations en ponte car elle implique la mise en commun de données à l'échelle internationale et la coordination des actions à entreprendre. D'où la nécessité de s'appuyer sur une règlementation internationale ou des Mémorandums d'entente.

Cette même dimension internationale se retrouve aux stades juvéniles. En effet, aux premiers stades de leur vie, les tortues dérivent sur de grandes distances le long des champs de courants océaniques (Carr, 1986). Chez certaines espèces, cette dérive passive ou semi-active peut d'ailleurs se dérouler à l'échelle d'un bassin océanique (Bolten 2003; Bowen et Karl, 2007; Boyle et al., 2009). Après cette phase pélagique, les juvéniles vont recruter sur des zones d'alimentation généralement côtières et peu profondes pour achever leur croissance et leur développement (Musick et Limpus, 1997). Les mécanismes qui motivent ce changement ontogénique sont encore totalement inconnus. La complexité de cette phase océanique réside dans le fait que l'accès à ces stades «dérivants» est extrêmement difficile. Ils sont d'ailleurs considérés comme les «lost years» – les années perdues – des tortues marines pour les chercheurs (Carr, 1952). De très récentes avancées technologiques en télémétrie satellitaire ont permis de mieux comprendre cette phase chez la tortue caouanne dans l'Atlantique nord (Mansfield et al., 2014), mais le mystère reste encore entier pour d'autres espèces.

La complexité de ce cycle de vie réside également dans l'échelle de temps concernée. La phase de «lost years» peut en fait durer une décennie (Musick et Limpus, 1997). Une fois que les juvéniles recrutent sur des habitats de développement côtiers, ils y resteront pendant plusieurs années avant d'atteindre la maturité sexuelle. Ces habitats pourront d'ailleurs varier au cours de leur développement en fonction des saisons (Naro-Maciel et al., 2007). La maturité sexuelle chez ces espèces intervient seulement après plusieurs décennies (e.g. la tortue verte: 25-30 ans; Limpus et Walter, 1980). Les adultes maintiendront ensuite leur cycle de migration de reproduction pendant des dizaines d'années, la longévité des tortues marines restant encore aujourd'hui un mystère. Le cycle de reproduction qui peut durer plus d'un demi-siècle, est également complexe car il n'est pas annuel et régulier comme chez la majorité des espèces. Par exemple, les femelles ne se reproduisent pas tous les ans (tous les 2-8 ans en moyenne; Lanyon et al., 1989). Cependant, l'année où elles se reproduisent, elles peuvent monter plusieurs fois pour pondre (3 fois en moyenne, mais le nombre de montées reste très variable, pouvant aller jusqu'à 11 fois sur une même saison; Hendrickson, 1958; voir discussion Chapitre 1, section 1), avant de retourner sur leur site d'alimentation auquel elles sont généralement fidèles, même si ce constat n'est pas toujours valable (Broderick et al., 2007; Schofield et al., 2010).

Si l'on ajoute à cela la difficulté technique à acquérir des données sur ces espèces (voir ci-dessus), la compréhension de toutes les interactions avec les différents écosystèmes qu'elles fréquentent et les variations environnementales qui influencent ce cycle (e.g. la température de surface de l'océan, Dalleau et al., 2012), on comprend bien que dans un contexte de biologie de la conservation, les tortues marines ne sont pas des modèles biologiques faciles à appréhender, comprendre et modéliser.

Objectif de la thèse

L'objectif de ce travail rentre dans cette démarche d'acquisition des connaissances sur une espèce menacée présente dans l'océan Indien occidental, la tortue verte. L'objectif global est d'être capable d'anticiper une situation de crise en fournissant des éléments essentiels de la biologie de la conservation de cette espèce aux gestionnaires locaux et régionaux. Dans un premier temps (Chapitre 1), ce travail vise à établir un document de référence sur l'abondance des tortues vertes femelles en reproduction dans le sud-ouest de l'océan Indien et les tendances sur le long terme des principales populations.

Dans un second temps (Chapitre 2), ce travail consiste à comprendre la structure des populations de cette espèce dans cette région du monde et d'estimer les relations qui existent ou non entre elles, mais aussi avec les populations des océans Atlantique et Pacifique.

Enfin, la conservation de ces espèces étant étroitement liée aux pressions extérieures qu'elles subissent, ce travail tente dans un troisième temps (Chapitre 3) de caractériser les pressions anthropiques et leurs impacts, et notamment ceux liés à la pêche, que subissent les tortues marines dans l'océan Indien occidental.

Une synthèse de l'ensemble de ce travail, associés aux autres études passées ou en cours sur ces espèces (Conclusion) permettra d'apporter une contribution scientifique significative à l'amélioration de la gestion de cette espèce, mais aussi d'anticiper des problèmes potentiels à venir sur la préservation de ces espèces fragiles et emblématiques. Pour finir, une réflexion sera proposée sur les priorités de gestion pour ces espèces dans l'océan Indien occidental et plus largement, dans la conservation régionale de la mégafaune marine.

CHAPITRE 1 – Evaluation des abondances et des tendances sur le long terme des populations de tortues vertes femelles en reproduction

Ce chapitre est décomposé en 2 sections et une synthèse.

La section 1 est constituée d'un article présentant une évaluation de l'abondance et de la tendance sur le long terme de la population de tortues vertes femelles se reproduisant à Mayotte.

Bourjea, J., Frappier, J., Quillard, M., Ciccione, S., Roos, D., Hughes, G., Grizel ,H., 2007. Mayotte Island: Another important green turtle nesting site in the South West Indian Ocean. Endangered Species Research 3, 273–282.

La section 2 est constituée d'un article soumis présentant un historique de l'exploitation ainsi qu'une évaluation de l'abondance et de la tendance sur le long terme de la population de tortues vertes femelles se reproduisant à Mohéli, Union des Comores.

Bourjea J., Dalleau, M., Derville, S., Beudard, F., Marmoex, C., M'soili, A., Roos, D., Ciccione, S., Frazier, J. submitted. Seasonality and increasing nesting of green turtles at Itsamia, Mohéli, Comoros, Submitted. Endangered Species Research.

La synthèse présente un bilan des abondances et des tendances sur le long terme des tortues vertes se reproduisant dans les principaux sites de reproduction du sud-ouest de l'océan Indien. Elle permet de se rendre compte de l'état de santé général de ces populations. Elle fournit également une série de recommandations nécessaires à l'amélioration des évaluations futures.

CHAPITRE 1 – SECTION 1 : L'ILE DE MAYOTTE : UN IMPORTANT SITE DE REPRODUCTION POUR LES TORTUES VERTES DANS LE SUD-OUEST DE L'OCEAN INDIEN

MAYOTTE ISLAND: ANOTHER IMPORTANT GREEN TURTLE NESTING SITE IN THE SOUTHWEST INDIAN OCEAN

Auteurs : Bourjea, J., Frappier, J., Quillard, M., Ciccione, S., Roos, D., Hughes, G., Grizel ,H.,

Année : 2007

Journal: Endangered Species Research

Numéro: 3

Pages: 273–282.

A retenir :

- Suivi journalier de la reproduction des tortues vertes entre 1998 et 2005 sur le site de Saziley
- Analyse des paramètres biologiques de la reproduction (évolution de la taille des individus, du nombre de pontes par femelle, du nombre de saisons de ponte…)
- Analyse de l'évolution de la tendance du nombre de nids de tortues vertes par un modèle ANOVA de spline lissé
- Les résultats indiquent que les paramètres de la reproduction de cette espèce sont standards et stables
- La population en reproduction sur le site de Saziley est estimée à 1545 (± 439) tortues par an
- La tendance de la population est stable entre 1998 et 2005
- Les données de Mayotte confirment que le sud-ouest de l'océan Indien est l'une des régions les plus importantes du monde pour la reproduction des tortues vertes

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Mayotte Island: another important green turtle nesting site in the southwest Indian Ocean

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ABSTRACT: Situated in the north of the Mozambique Channel, Mayotte is the easternmost island of the Comoros Archipelago. From 1998 to 2005, Grande Saziley beach was monitored daily for green turtle *Chelonia mydas* nesting activity. Track surveys were monitored daily on 5 other adjacent beaches. Although nesting occurs throughout the year, nesting seasonality begins at the end of the wet season and intensifies during the dry season to reach an average nesting peak in June. In order to estimate the number of females nesting in the Saziley site and population trends over the study period, incubation success and number of nests per female and per season were estimated at 0.77 (±0.05 SD) and 3.03 (±0.37) respectively. With an average of 1545 nesting turtles per year (±439), the change in nesting numbers over the study period was so small that the population can be regarded as stable, with an estimated annual mean growth rate of 0.912, confirmation that this population is both stable and in good health. Added support for this argument is demonstrated by the fact that the annual carapace size distribution of nesting females is stable, meaning that the nesting green turtle population of Mayotte is not ageing or rejuvenating. After due consideration of data on other nesting sites in the southwest Indian Ocean, the data from Mayotte emphasizes the fact that the green turtle is not an endangered species in this region. Even if it is still illegally exploited and alterations occur in their different habitats, the green turtle populations of this region seem to have successfully survived all threats during the past century.

KEY WORDS: *Chelonia mydas* · Population assessment · easonality · Nesting trend

INTRODUCTION

The green turtle *Chelonia mydas* is found circumglobally in subtropical waters and is a highly migratory, long-lived species with delayed sexual maturity and high adult survival but low hatchling survival. The species has had a long history of human exploitation in all oceans, with some stocks now extinct, others in decline (Frazier 1980, Witzell 1994) and some stocks showing significant restoration following dedicated conservation effort (Balazs & Chaloupka 2004). However, in many areas the green turtle is now regarded as an endangered species due to overexploitation of eggs and adults on nesting beaches, by catches in fisheries and alterations in both nesting and feeding habitats (World Conservation Union [IUCN] Red List, Seminoff 2004). The southwestern Indian Ocean (SWIO) remains an important nesting and feeding ground for

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green turtles (Hughes 1973, Frazier 1975 1985, Le Gall et al. 1985, Mortimer 1985, Le Gall 1988, Lauret-Stepler et al. 2007) even if, over the past few centuries, overexploitation and habitat destruction have resulted in the decrease and local extinction of a few populations in this region (Frazier 1975, Rakotonirina & Cooke 1994). Sea turtle activities in many of the islands in the region are well monitored, especially on Europa, Tromelin, Grande Glorieuses (Hughes 1974, Le Gall et al. 1985, Lauret-Stepler et al. 2007), Comoros archipelago and Mayotte (Frazier 1985), Iranja island (Bourjea et al. 2006) and Reunion Island (Ciccione & Bourjea, 2006). This region of the world is of significant interest to managers and scientists not just because it harbours large stocks of sea turtles, especially green turtles, but also because molecular evidence suggests a split between the green turtle population from the northern Mozambique Channel, being most closely related to the Indo-Pacific genetic stock and the population from the southern Mozambique Channel most closely related to the Atlantic stock (Bourjea et al. 2007).

The technique most commonly used to assess population size and trend is to count the number of clutches laid in a season (Schroeder & Murphy 1999), but track counts can also be used as an index of female abundance and change at the nesting sites, assuming that the mean number of tracks per female per season remains relatively constant through time (Seminoff 2004). However, accurate population assessment is more difficult when a population nests on many beaches and all year long. In such cases, labour intensive surveys are required but unfortunately quite often impossible to organize. Three options for population assessments are available; either limiting the counts to a small part of the year, for instance peak nesting periods only, or selecting specific sites to act as index beaches, or both in combination. In the case of key index beaches the biological data and trends are extrapolated to the rest of the island.

Mark-recapture programmes are indispensable for understanding nesting behaviour typical within a region, and are useful for comparing species behaviour on a site, region or ocean basis. Mayotte is the easternmost island of the Comoros Archipelago. It is an exceptional rookery for nesting green turtles comprising numerous suitable nesting sites (Frazier 1985) spread along the entire island. Two species of sea turtle are known to nest on this island: hawksbill *Eretmochelys imbricata* and green turtle, the latter being the most abundant. In addition to global protection laws, the Directorate of Agriculture and Forestry (DAF) in association with the Department Organization of Mayotte (CDM) strengthened the protection of sea turtles in 1994. This was done by developing specific protection and conservation plans for the entire island, with special features for the 2 sites(Saziley and Moya) most frequented by green turtles.

The fundamental goal of our study was to assess green turtle nesting activity at the Saziley rookery and hence, to analyse changes in 2 population health indicators that remain fundamental for conservation measures: the number of nests and carapace length. We describe here the design and implementation of the survey regime which allowed us to estimate these nesting indices.

MATERIALS AND METHODS

Study site. Mayotte Island (15° 33′ S, 54° 31′ E) is one of the islands of the Comoros archipelago, situated in the north of the Mozambique Channel, between Madagascar and Mozambique (Fig. 1). This 374 km^2 island is an Overseas Département of France which, in 2005, had 170 beaches that were suitable for turtle nesting (BDTopo Mayotte). Some of the beaches are accessible to residents who use the beaches for recreational or ecotourism purposes. Saziley, however, is a protected area where tourism is controlled and turtles are monitored by special staff from the Department of Mayotte. Saziley has 6 discrete beaches with 2239 m of sandy beach suitable for nesting. The largest beach is Grande Saziley; this site can be reached on foot requiring a 1 h walk or a 30 min journey in a motorized boat.

Data collection. Since 1 January 1998, 4 teams of 2 nature guards patrolled the beach of Grande Saziley beach every night of the year. For each nesting green turtle found, they (1) made biometric measurements (curved carapace length, CCL), (2) noted aborted digging attempts or successful nests and (3) tagged each turtle with a classic 'Monel' metal tag (1005-46 Monel tag 035 MO) or (4) recorded tag numbers of previously inserted tags.

Track surveys on nesting beaches are often used to assess nesting sea turtle populations (Schroeder & Murphy 1999). These utilise the fact that each time a female sea turtle emerges from the water to attempt nesting, called 'nesting activity' (Godley et al. 2001), it creates a set of tracks on the sand, one ascending and the other one descending to the sea. By counting all the tracks on the beach, and dividing by 2, it is possible to infer how much nesting activity occurred on a particular beach in any given period. Since 1 January 1998, the team has patrolled each of the 6 beaches at the Saziley site every morning and recorded the number of nesting turtle tracks on the assigned beach to determine nesting activity. Once recorded, the nature guard cancels the tracks to avoid double-counting the next day.

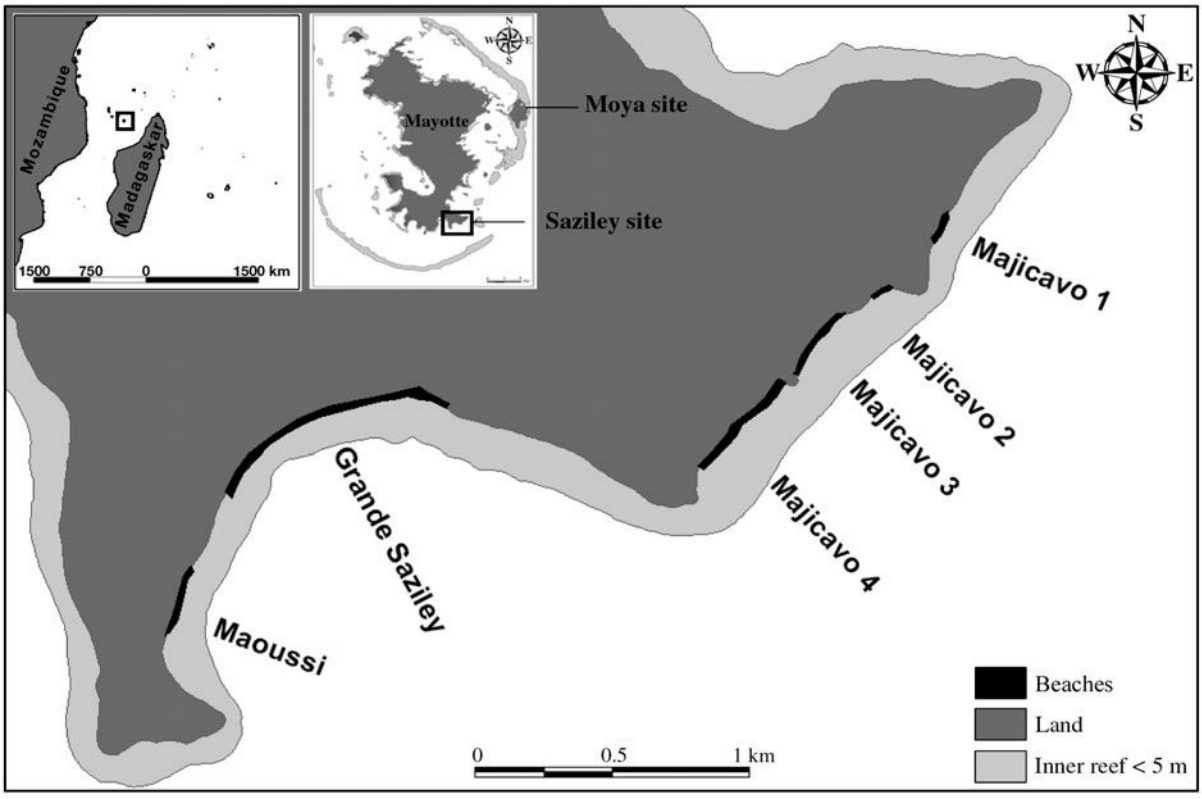

Fig. 1. Saziley site on Mayotte (15°33′S, 54°31′E) illustrating green turtle nesting beaches. This site consists of 6 beaches (Maoussi, Grande Saziley and Majicavo 1, 2, 3 and 4). Only Grande Saziley is monitored every night for tagging, carapace measuring, track counting and nesting activity of female green turtles. The other 5 beaches are only monitored in the morning for tracks

Calculation of nesting indices. The calculation of the following nesting indices is based on the daily mark-recapture monitoring (due to the large number of gaps and inadequate coverage, data from 1994 to 1997 were not used in the calculation of nesting indices).

Within season renesting interval: Green turtles often lay more than one clutch of eggs during a nesting season. We assessed nesting intervals using a compilation of all renesting intervals (in number of days) recorded at Grande Saziley.

Nesting success: Turtles do not lay eggs during every nesting emergence and can abort nesting efforts at a number of different stages of the nesting process, returning to the sea to re-emerge the next night or on some subsequent night. In this study, we calculated the nesting success $\hat{r}$ for Grande Saziley as the ratio between the number of activities observed (NA_{obs}) and the number of nests observed (NN_{obs}) in a nesting season:

$$\hat{r} = \frac{NA_{obs}}{NN_{obs}} \quad (1)$$

Numbers of nestings per female: We calculated the mean number of nestings per female and per season $\hat{m}$ as the ratio between NA_{obs} and the total number of individuals identified by a Monel tag and observed on a site (NI_{obs}) within the nesting period:

$$\hat{m} = \frac{NA_{obs}}{NI_{obs}} \quad (2)$$

Total number of nesting females: For the 6 nesting beaches surveyed over the period, we estimated the total number of tracks (TNT) with the monthly assessed data. The total number of nesting females (TNF) was then calculated using $\hat{r}$ and $\hat{m}$ as follows:

$$TNF = \frac{TNT \times \hat{r}}{\hat{m}}$$

Trend analysis. We compiled the nest abundance time series for the Saziley site (1 of the 2 major green turtle nesting sites of Mayotte) based on the nesting indices determined with tagging-recapture data. We then estimated the underlying time-specific trend in Mayotte nest abundance over the study period using a smoothing spline ANOVA model (Chaloupka et al. 2007) implemented in R 2.2.0 (Ihaka & Gentleman 1996). This non-parametric approach uses the data to determine the smooth trend with 95% Bayesian confidence curves without assuming any specific functional form. We as-

sumed that the fit was reasonably linear, so an estimate of the linear trend from a linear regression was accounted for by autocorrelation and weighted variance of the smooth estimate. The advantage of this approach is that it enables robust estimation of the mean growth rate. We used all the data in natural log form.

Lastly, we investigated the expected size distribution of female green turtles nesting each year on Grande Saziley beach using schematic box plot summaries, as long-term size distribution data are available for this site only.

Additional information. We estimated and graphed the average monthly minimum and maximum temperatures and the average monthly rainfall. We obtained historical meteorological data from the Météo France weather station based at Mayotte airport which provided us with data from 1 January 1998 to 1 January 2006.

RESULTS

Monitoring, nesting indices and seasonality

The nature guards have monitored the nesting turtle activity on 6 beaches of Saziley site (Fig. 1) daily since 1998. For Grande Saziley beach, the guards were active on 91% of the days in this period, counted 13415 tracks corresponding to 5167 nests, tagged and measured 3090 female green turtles and recorded 6025 recaptures (Table 1). For the 5 other beaches (Fig. 1), the guards surveyed > 85% of the total number of days in the period and counted 28993 tracks. Because the guards surveyed the beaches in the morning, they did not conduct tagging on these 5 beaches and they did not collect data on aborted digging attempts or successful nests.

Having compiled all the data on tracks, we established the temporal distribution of the green turtle tracks for the 8 seasons from January 1998 to December 2005 (Fig. 2). The peak of nesting activity was during the austral winter, in June, with an average of 715 tracks counted over the 6 beaches in this month. It should be noted that 90% of the tracks occurred between 5 February and 28 October and 95% between 11 January and 15 December.

For the within-season renesting interval, we performed a compilation of all renesting intervals recorded at Grande Saziley during the 1998 to 2005 periods (Fig. 3). Three modes were identified (Fig. 3). The first one, between 0 and 7 d is centred on 2 d and

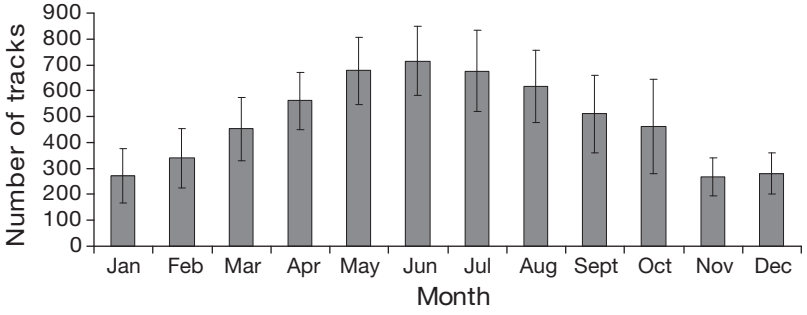

Fig. 2. Mean number of tracks (±SE) recorded each month between January 1998 and December 2005 for the 6 Saziley site beaches. Months with >10 consecutive days of missing data were not included in the calculation

Table 1. Summary of the monitoring (from 1998 to 2005) on Grande Saziley beach: number of taggings and recaptures, number of nests and tracks counted and the respective equivalent effort in day monitoring (monitoring effort was the same for both 'No. of quests' and 'No. of tracks'). TNT (total number of tracks) was estimated filling in the missing data by a 10 d extrapolation based on the sampling rate; $\hat{r}$ (nesting success) $\hat{m}$ estimated with the tagging recapture data and the number of nests recorded per female and$\hat{m}$ (number of nestings per female) were. TNF (total number of females) was estimated with the calculated nesting indices

Year	Tagging	Recapture	No. of nests	No. of tracks	Effort (d)	TNT	$\hat{r}$	$\hat{m}$	TNF
1998	347	939	779	1837	338	1956	0.82	3.66	438
1999	398	862	787	1781	320	1957	0.82	3.06	524
2000	265	576	444	1205	343	1280	072	3.48	263
2001	617	932	854	2335	314	2723	0.76	2.65	779
2002	286	481	334	1230	292	1592	0.69	2.69	408
2003	473	820	750	1788	338	1964	0.78	2.88	536
2004	305	647	587	1487	353	1527	0.83	3.04	416
2005	399	768	632	1752	358	1788	0.77	2.73	502
Total	3090	6025	5167	13415					
Average							0.77	3.03	483
SD							*0,05*	*0,37*	148

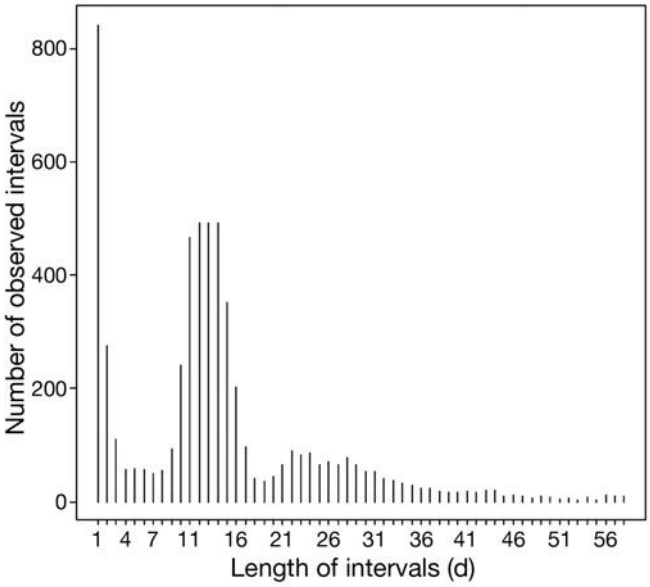

Fig. 3. Time intervals separating consecutive use of nests by Grande Saziley green turtles based on tag recoveries between 1 January 1998 and 31 December 2005

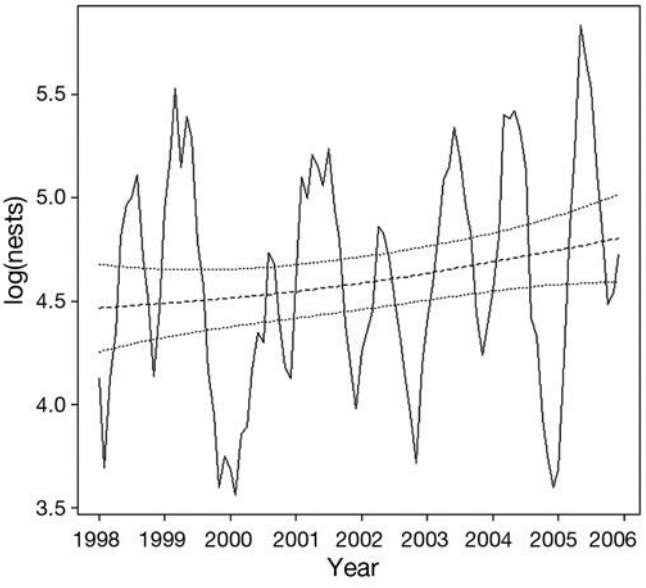

Fig. 4. Long-term trend of green turtle nesting abundance for Grande Saziley beach (Mayotte). Solid line: recorded green turtle nesting from 1998 to 2005; central dotted line: estimated underlying trend in nest abundance for the same period; lower and upper dotted lines: 95% Bayesian confidence curves

clearly belong to females that aborted their first nesting attempt and came back 1 to 7 d later (n = 1451). We noted that 25% of the female green turtles aborted their first nest and came back the following day. The second mode is centred on 12 to 14 d (n = 3105), meaning that turtles nest again after an interval of 12 to 14 d. The third lesser mode is centred on 25 to 28 d (n = 1009) and represents the third nest of the same turtle during a nesting period. Even if in some cases, renesting occurs more that 150 d after the first emergence, no other mode can be clearly identified.

Over the study period, we recorded the nesting activities of 90 turtles over several separate seasons. The interval between 2 nesting seasons was estimated at 3 yr (SD = 1). We also estimated a nesting success ($\hat{r}$) of 0.77 (±0.05 SD) and a number of nests per female per season ($\hat{m}$) of 3.03 (±0.37; Table 1). Based on the estimation of $\hat{r}$ and $\hat{m}$, we estimated that an annual average of 483 females (±148, Table 1) nested at Grande Saziley, an 800 m long black sandy beach, suggesting an annual average of 600 turtles per kilometre of beach.

Long-term nesting trend and trend in size of nesting females

The distribution of nest abundance over the study period (Fig. 4) shows the annual periodicity of the nesting period identified in Fig. 2. Variations in the estimated nesting peak appear year to year, with the highest peak in 2005 (n = 342 nests in May). In order to establish the trend over this 8 yr period, we implemented a smoothing spline ANOVA model (Chaloupka et al. 2007). The long-term trend in nest abundance was assessed from 1998 to 2005 and appeared to increase over the period. This increase is verified by the estimated mean growth rate δ = 0.912.

Box plot summaries of the annual size distribution of green turtles nesting over the 8 yr sampling period on Grande Saziley beach are shown in Fig. 5. The overall median for the 8 yr sampling period is shown by the solid horizontal bar, which is 108 cm straight carapace length (CCL). The size distribution for each annual sample fluctuates around the overall median without any obvious long-term trend.

DISCUSSION

Nesting indices

The nesting activity on the 6 beaches was intense. Also intense was the tagging-recapture effort over Saziley beach, with > 91% of the days monitored (Tables 1 & 2); this allowed us to estimate what we believe reflects the biological reality of the different nesting indices.

Green turtles lay several times over a reproductive season, but the average time between consecutive

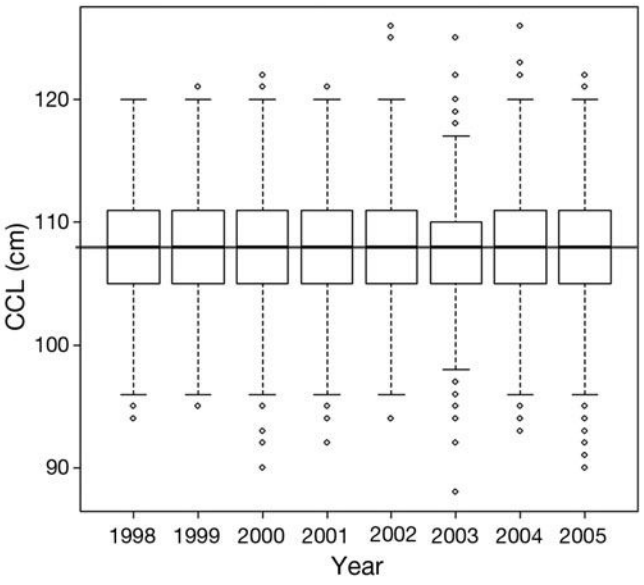

Fig. 5. Box and whisker plot summary of the annual CCL (curved carapace length) distribution of green turtles nesting over the 8 yr sampling period on Grande Saziley beach. Thick horizontal line in each box: 50th percentile (median) of carapace size for each annual sample; upper and lower boundaries of each box: 75th and 25th percentiles; top and bottom of the whiskers: 90th and 10th percentiles; points above the 90th percentile: extreme outliers. Horizontal line: overall median (108 cm CCL) for the 8-yr sampling period

nesting emergences varies from population to population, with a mean global renesting period of 12 d (range: 10 to 17 d; Miller 1997). Our study based on more than 13400 nesting records shows that between-nesting periodicity in Mayotte falls within the known range for green turtles. Records indicate a period of 12 to 14 d for the second nest. Lesser peaks roughly correspond to multiples of 12 to 14 d. Equivalent data were found by Mortimer & Carr (1987) in Ascension Island, and in the Indian Ocean (Le Gall 1988). Furthermore, several authors agree that the first peak, centred on 2 d (Fig. 3), indeed all turtles that came back before 8 d are those returning after an aborted attempt to nest (Balazs 1980, Le Gall 1988). Green turtles are also known to lay as many as 11 clutches in one season (Hendrickson 1958). In our study, although one female emerged 15 times over the nesting season, laying 10 nests in 2001, the average green turtle nests 3 times ($\hat{m}$ = 3.03 ± 0.37 SD) in a season. Equivalent results were found in Ascension Island ($\hat{m}$ = 3.0; Mortimer & Carr 1987), in Tortuguero, Costa Rica ($\hat{m}$ = 2.8; Carr et al. 1978) and in the Indian Ocean on Tromelin and Europa islands ($\hat{m}$ = 3.5 and $\hat{m}$ = 2.8, respectively; Le Gall 1988).

Nesting success on Saziley beach ($\hat{r}$ = 0.77 ± 0.05 SD) appears higher than some other nesting sites ($\hat{r}$ = 0.66 ± 0.0095 at Europa, Le Gall 1988; $\hat{r}$ = 0.56 ± 0.004 at Tromelin, Le Gall 1988; $\hat{r}$ = 0.33 ± 0.08 at Ascension Island, Godley et al. 2001). Limpus et al. (2003) showed a very high variability in the nesting success on Raine Island (Australia) and proposed that the nesting success is influenced by various parameters such as nesting density on the beach, and rain. These data illustrate the variability that can occur in nesting success for turtles attempting to nest in coralline sand.

This high variability does not occur at the Saziley nesting site, where nesting success remained the same over the years studied (Table 1). It should be noted that the beaches at this site are composed of a mixture of coralline (white) and volcanic (black) sands, ranging from > 90% of coralline sand at Majicavo 1 to > 90% volcanic sand at Grande Saziley beach (Fig. 1).

We assessed remigration intervals using the data collected on 90 turtles recaptured during this 8 yr study on Grande Saziley beach, Europa and determined that the most frequent remigration interval for the green turtle is 3 yr; this agrees with the most commonly

Table 2. Summary of the monitoring (1994 to 2005) on 5 beaches of the Saziley site: number of tracks counted and the equivalent effort in day monitoring. TNT (total number of tracks) was estimated filling in the missing data by a 10 d extrapolation based on the sampling rate. TNF (total number of females) was estimated with the calculated nesting indices on Grande Saziley

Year	Maoussi		Majicavo1		Majicavo2		Majicavo3		Majicavo4		TNT	TNF
	No. of tracks	Effort (d)	No. of tracks	Effort (d)	No. of tracks	Effort (d)	No. of tracks	Effort (d)	No. of tracks	Effort (d)		
1998	596	290	143	238	517	295	821	295	1085	296	3699	945
1999	668	318	155	320	401	321	713	321	881	321	3095	791
2000	787	334	139	333	439	334	606	334	814	334	3027	774
2001	1048	302	477	306	873	307	1215	306	1670	305	6403	1636
2002	539	280	148	280	394	280	688	279	766	279	3346	855
2003	950	312	455	316	783	316	1008	316	1275	317	5077	1297
2004	854	331	242	329	470	333	781	332	1021	333	3634	929
2005	896	311	275	265	767	324	1123	324	1510	324	4976	1272

observed multi-annual renesting interval for this species (Le Gall et al. 1985, Miller 1997, Troëng & Chaloupka 2007). The multi-annual recapture rate on Grande Saziley, a beach flanked by several other beaches, is low (2.4% of the total number of tagged turtles), and these results are similar to those obtained by studies on many other green turtle populations. Le Gall et al. (1985) found a similar rate (3.82%) for a beach on Europa Island in the south of the Mozambique Channel. However, Le Gall et al. (1985) also found a recapture rate of 2.17% for Tromelin Island, which, in contrast to Europa and Mayotte, has only a single beach, meaning that green turtle fidelity to a specific beach is not necessarily dependent on the presence of other beaches adjacent to it.

Total nesting females on 6 beaches at Mayotte

Based on the estimated nesting indices $\hat{r}$ and $\hat{m}$ calculated on Saziley beach and on the daily track monitoring since 1998 on 6 beaches of Mayotte, it was possible to estimate the annual number of green turtle females nesting on these 6 beaches: 1545 (± 439 SD) nesting turtles (calculation based on Tables 1 & 2). Even if the nesting success on Saziley beach ($\hat{r}$ = 0.77 ± 0.05) and the number of nests per female ($\hat{m}$, = 3.03 ± 0.37) do not vary very much from year to year on Grande Saziley, the estimation of the number of green turtle females nesting on these 6 beaches should be considered as an order of magnitude, not as the field reality. We need to consider that there are numerous parameters that were not taken into account for the calculation, such as site fidelity, tag losses, variability in the remigration intervals and weak synchrony in the remigration behaviour.

The Saziley site is one of the two main nesting sites of Mayotte. The other is the site of Moya (Fig. 1), where the estimated number of nesting turtles seems to be similar to that on Grande Saziley beach, meaning that > 2000 turtles nest on these 2 sites. Even if the other beaches around Mayotte do not have the same level of nesting green turtles, with a total of 170 beaches suitable for nesting sea turtles (BDTopo Mayotte), Mayotte Island represents another very valuable colony of green turtles in the SWIO. In this region, it has been estimated that Europa Island hosts a colony of 3000 to 10 000 females yr^{-1},Tromelin Island hosts 1000 to 3000 (Le Gall et al. 1986), Moheli in the Islamic Republic of the Comores 1000 to 3000 (Hughes, pers. comm.), Aldabra 6000 to 8000 (Mortimer 1985) and a portion of Grande Glorieuse Island hosts 1480 ± 480 (Lauret-Stepler et al. 2007). Considering the other nesting sites in the Seychelles archipelago (Cosmoledo, Amirantes), Mozambique (Bazaruto, Primeiras and Segundas), all the east coast of Africa and Madagascar and the St Brandon Shoals of Mauritius, it is clear that the SWIO is an extremely important region for nesting green turtles.

Temporal distribution of nesting effort

Although nesting occurs throughout the year, nesting seasonality on Mayotte begins at the end of the wet season, intensifies during the dry season, with an average nesting peak in June and ends at the beginning of the new wet season (Figs. 2 & 6). Nesting seasonality patterns on Mayotte are therefore similar to those of the majority of green turtle colonies studied worldwide. Many colonies have nesting throughout the year with a distinct nesting peak at a specific season (see for example Bjorndal et al. 1999, Chaloupka 2001, Godley et al. 2002).

Within the SWIO, different seasonality patterns were recorded, with nesting peaks occurring for Mayotte during the dry season in the north of the Mozambique Channel (Grande Glorieuse island, Lauret-Stepler et al. 2007; Iranja Island, Bourjea et al. 2006) and during the wet season for the south of the Mozambique Channel (Europa Island; Lauret-Stepler et al. 2007). The SWIO green turtle seasonality pattern seems to be correlated with genetic structuring in the region: there is compelling genetic evidence that green turtles nesting in the rookeries of the south Mozambique Channel (SMC) and those nesting in the north Mozambique Channel (NMC) belong to separate genetic stocks (Bourjea et al. 2007).

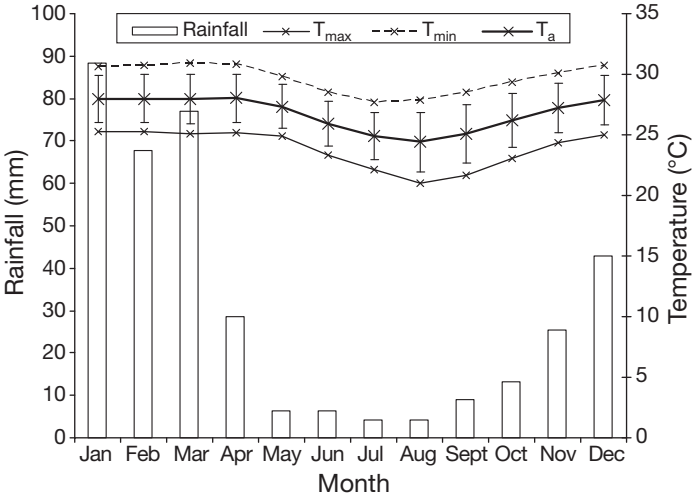

Fig. 6. Monthly mean of maximum (T_{max}), minimum (T_{min}) and average air temperature T_a and rainfall in Mayotte (1 January 1998 and 31 December 2005). SE is given for T_a. Data were obtained from Météo France for the east coast of Mayotte

However, the Tromelin rookery off the east coast of Madagascar and part of the NMC stock show a seasonality pattern where peak nesting occurs during the wet season, as for rookeries from SMC stock, meaning that other external factors could be involved (Lauret-Stepler et al. 2007). Based on data on Australian green turtle rookeries, Limpus et al. (2003) proposed that this variability in timing of the nesting season probably results from the interaction of a number of factors which are thought to include the genetic origin of the population, but also the temperature regime of the rookery and the climate of the feeding grounds providing turtles to the rookery. A large regional analysis of nesting seasons based on sea surface temperature (SST), air temperature, and rainfall variation is clearly needed; these data should, however, be procured not only from island but also from mainland rookeries (i.e. Madagasacar, East African coast).

Long-term nesting trend

Changes in nesting numbers over the study period are low, with an estimate mean growth rate of 0.912 (Fig. 4). Sea turtles have been protected in Mayotte since 1994, and the time series analysis confirms that protection of nesting sites does have a positive impact on nesting populations, as has been observed in other studies (Chaloupka & Limpus 2001, Balazs & Chaloupka 2004, Troëng & Rankin 2005). Where committed conservation measures have been introduced, the increase in nesting numbers has been dramatic, for instance on Heron Island, Australia (Chaloupka & Limpus 2001), Hawaii, USA (Balazs & Chaloupka 2004), or Tortuguero, Costa Rica (Troëng & Rankin 2005). This suggests that the population of green turtles in Mayotte before the implementation of conservation measures was not over-exploited. Added support for this argument is that the overall median for each annual sample of CCL was stable over the study period (Fig. 5), meaning that the nesting green turtle population of Mayotte is not ageing or rejuvenating: a sign that this population is both stable and in good health. This argument is only valid if we assume that there is no significant change in the size of first maturity over the study period.

However, as shown in other studies (Le Gall 1988, Hays et al. 1999, Solow et al. 2002), the high inter-annual variability in the number of nests can render the interpretation of trends for the different sites difficult, especially over short-term study periods. Variability in the remigration intervals and weak synchrony in the remigration behaviour of the nesting individuals can account for the inter-annual variability in the number of individuals seen in a colony (Solow et al. 2002). Environmental factors such as cyclones and El Niño Southern Oscillation associated with warmer sea surface temperatures were found to influence the number of individuals migrating to their nesting sites, causing this high inter-annual variability (Limpus & Nicholls 1988, Solow et al. 2002, Ross 2005).

Status of the green turtle in the SWIO

The data collected on Mayotte (Roos et al. 2005, Taquet et al. 2005, present study) showed astonishing abundance of foraging and nesting green turtles, and since monitoring started, data on nesting green turtles from other nesting sites in the SWIO have shown stability or significant increases (Mortimer 1985 and Lauret-Stepler et al. 2007 suggest that this has been achieved through long-term conservation measures). Thus, it appears that the green turtle is not an endangered species in this region.

This means that following the near collapse of large green turtle rookeries in the early twentieth century (e.g. Aldabra and Europa), the now large green turtle population of the SWIO seems capable of supporting the present level of exploitation.

However, sea turtles are still illegally exploited and by-caught in the SWIO, mainly in Madagascar (Rakotonirina & Cooke 1994), the Comoros archipelago and the east African coast. The question is: What will happen if exploitation increases or there are dramatic alterations in both nesting and feeding habitats? In the case of Mayotte, with the large increase of tourism on this island (from 21 000 tourists in 1999 to 39 000 in 2005; data from Institut National de la Statistique et des Etudes Economiques - INSEE) and demographic growth (130 000 inhabitants in 1997 to 185 000 in 2006; data from INSEE), negative impacts on the coastal environment, and thus on sea turtle nesting and foraging habitat, will inevitably occur. Conservation measures seem to be the only way to regulate those human activities on the coast that could influence the resident and nesting populations of sea turtles. Furthermore, in addition to ensuring the preservation of sea turtles, if these conservation measures are well implemented they can have a positive economic impact on this small island with limited economic resources.

Another point of concern is that, even if the recent results on population monitoring in the main nesting sites of the SWIO are positive, it remains important to increase the monitoring in other smaller nesting sites such as Madagascar (Bourjea et al. 2006) or along the east coast of Africa. This is essential because small rookeries play an important role in the genetic diversity of this species in a zone that has populations from the Atlantic and from the Indo-Pacific Oceans (Bourjea

et al. 2007). More studies need to be carried out on foraging grounds in order to determine conservation measures where necessary. Turtles nesting on Mayotte seem to feed on the east African coast, mainly Tanzania and Kenya (J. Bourjea pers. comm.) where sea turtles are still threatened by harvesting and by-catch in small-scale and commercial fisheries (Bourjea et al. 2007).

In conclusion, we believe that the results of this study on Mayotte confirm the existence of yet another stable to increasing population of green turtles protected in the SWIO which, added to those studies on other formally protected rookeries with stable or growing populations of green turtles nearby, further confirm our conviction that the region represents one of the world's most valuable green turtle stocks. The data collected through careful monitoring and accurate assessment should be of great value when the IUCN next reviews the global status of this valuable species.

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SEASONALITY AND INCREASING NESTING OF GREEN TURTLES AT ITSAMIA, MOHÉLI, COMOROS

Auteurs : Bourjea J., Dalleau, M., Derville, S., Beudard, F., Marmoex, C., M'soili, A., Roos, D., Ciccione, S., Frazier, J.

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A retenir :

- Historique de l'exploitation des tortues marines à Mohéli
- Suivi journalier de la reproduction des tortues vertes entre 1999 et 2007 sur 5 plages d'Itsamia à Mohéli
- Analyse des paramètres biologiques de la reproduction (nombre de traces et nombre de pontes par femelle)
- Analyse de l'évolution sur le long terme de la tendance du nombre de nids de tortues vertes par un modèle additif mixte (GAMM) et par décomposition de la série temporelle par un modèle de lissage LOESS (STL)
- Les résultats indiquent que les paramètres de la reproduction de cette espèce sont standards et stables
- La population en reproduction sur les plages d'Itsamia est estimée entre 3000 et 5000 tortues par an
- La tendance de la population est à la forte croissance depuis 1999 (+24% par an)
- Ces résultats montrent que la gestion des tortues marines par les communautés locales peut être extrêmement efficace.

Seasonality and increasing nesting of green turtles at Itsamia, Mohéli, Comoros

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Keywords: Green turtle; nesting; seasonality; trend; Comoros; Mohéli

Running Head: Nesting green turtles at Moheli

ABSTRACT (250 words)

This study on green turtles (*Chelonia mydas*) was conducted at Moheli Island, Union of Comores, South West Indian Ocean (SWIO). Five contiguous beaches near Itsamia Village, in the SE of the island were monitored daily for nesting activity over an eight and a half year period (January 1999 – June 2007), and for nesting success over a seven-year period (2000 – 2006). Nesting occurred year round, and peaked in the austral winter, from March through August, with the highest values in May: the average for the month was 2265 nesting attempts (SD =994, n=9). During the seven-year period 63164 successful nestings were reported, and a total of 69630 successful nestings were estimated when values from missing data were included. The average rate of nesting success as 0.49 (SD=0.04, n=7). Using the estimate of 3.03 successful nestings per female per season, the estimated number of nesting females per year varied from 924 in 2000 to 5827 in 2005. There was marked growth in nesting activity over the study period, as indicated by STL and GAMM analyses, with an increase of 226% (ranging from 143%–391% with 95% confidence intervals) from 1999 to 2006. Hence, the Itsamia beaches have one of the largest nesting populations, with a higher rate of increase than any other site in the SWIO. Long-term protection of the beaches and offshore waters by the Itsamia community, despite several years of intense exploitation by people from other islands, is reasoned to be the primary explanation for these remarkable figures.

Introduction

Situated at the Northern end of the Mozambique Channel, the Comoro Archipelago is composed of 4 main islands: Grande Comore (or "Ngazidja"), Anjouan (or "Ndzouani"), Mayotte (or "Maoré"), and Moheli (or "Mwali"). Grande Comore is the largest, and hosts the capital Moroni; Anjouan has the greatest human population; and Moheli is the smallest. Mayotte is a French overseas territory, while the other three islands form the Union of Comoros. Initial field studies on marine turtles in Comores were carried out between 1972 and 1985 (Frazier 1975; 1980; 1982; 1984; 1985; Hughes 1982; Fretey & Fourmy 1996), after which there was a lull for nearly twenty years. Although Frazier (1985) reported no nesting on Grande Comore or Anjouan, he estimated that about 2000 green turtles nested annually on Moheli, with at least 36 beaches showing nest spoor out of a total of 92 beaches suitable for nesting. At the same time, almost four decades ago, Mayotte was thought to host less than 600 annual nesters with 19 beaches showing signs of nesting (Frazier 1985). However, more recently it has been estimated that more than 2000 females nest annually on just the two most important beaches of Mayotte (*i.e.* Saziley and Moya), and a total of more than 3000 nesters per year are thought to use 82 beaches out of 170 suitable nesting beaches on this island (Bourjea et al. 2007a).

The consumption of turtle meat is generally common on Grande Comore and Anjouan, but the habit varies between different villages on Mayotte and Moheli. Although nearly all inhabitants of Comoros are Muslim, the consumption habits depend on religious beliefs, demography and ethnic origin of the village (Lilette 2007). For example, at Itsamia, on the south east of Moheli, the community is Islam shafeite, with a belief system that forbids the consumption of animals that live in two different worlds. Hence, marine turtles that live in the water and nest on land are "haram" (*i.e.* "forbidden" and /or "sacred") and turtle meat is not consumed, and reportedly never was. However, the introduction of motorised boats to the Comores in the early 1980s allowed the beaches of Itsamia to be easily reached by people from Anjouan and Grande Comore, which resulted in the active exploitation and trade of turtles and their meat, especially reproductive females butchered on the beaches of Itsamia (Lilette 2007).

In 1991, in response to the outside disturbance – especially the intense, uncontrolled exploitation of turtles, the inhabitants of Itsamia founded the Association pour le Développement Socio-Economique d'Itsamia (ADSEI – Association for the Socio-Economic Development of Itsamia). Through ADSEI they took measures to stop turtle poaching at Itsamia, relying on the fact that marine turtles are protected by national legislation, as well as by international conventions of which Comores is a signatory. This local initiative has been coupled with economic and socio-political development of the village; motivated by the protection of marine turtles,

74 international organisations have provided financial and technical support to construct a communal building (the
75 Turtle House) and tourist bungalows. Of particular importance, in 1999 a partnership between ADSEI, Kelonia
76 (the Marine Turtle Centre of Reunion Island) and Ifremer (Institut Français de Recherche pour l'Exploitation de
77 la Mer) was created with two primary goals: to protect the threatened marine turtles through local awareness
78 campaigns, and to develop income-generating activities such as nature tourism. This partnership has also
79 included the monitoring of the five contiguous nesting beaches that are in the immediate vicinity of Itsamia, on
80 the eastern extreme of the island (Fig. 1), a project that began in 1999 and continues to date.
81
82 The green turtle *Chelonia mydas* is a highly migratory, long-lived species with delayed sexual maturity and
83 high adult survival, but low survival in the early life stages. This species is found circumglobally in tropical and
84 subtropical waters; and in many areas the green turtle is now regarded as an endangered species. It is listed on
85 the International Union for Conservation of Nature (IUCN) Red List (www.iucnredlist.org), due primarily to
86 overexploitation of eggs and adults on nesting beaches, as well as bycatch in fisheries and perturbation to both
87 nesting and feeding habitats (Seminoff 2004). Indeed, there is considerable evidence of significant population
88 declines of green turtles over the past few centuries, especially in the Indian Ocean region, most of which is
89 thought to be due to overexploitation and destruction of nesting and foraging habitats (Frazier 1974, 1980;
90 Ciccione & Bourjea 2006). Nonetheless, the South West Indian Ocean (SWIO) has hosted some
91 of the world's most important nesting and feeding grounds for green turtles (Frazier 1971, 1975, 1984, 1985;
92 Hughes 1973; Le Gall et al. 1986; Le Gall 1988). This region – defined here as the waters bounded by eastern
93 coast of Africa extending from Kenya to South Africa and east as far as 60° E – nowadays includes major green
94 turtle nesting areas such as Europa and Tromelin Islands (Lauret-Stepler et al. 2007), Aldabra Atoll (Frazier
95 1971, 1984; Mortimer 1985, Mortimer et al. 2011a), and Mayotte (Bourjea et al. 2007a), where each island/atoll
96 regularly hosts thousands of annual nesters. Wallace et al. (2011) identified a single regional management unit
97 (RMU) for green turtles in the SWIO, but recent genetic research showed that this region hosts at least 3
98 different genetic management units for this species (Bourjea et al. 2007; submitted). Therefore, population
99 evaluation on other islands of the SWIO – particularly those like Moheli that are thought to host large nesting
100 populations – is essential for estimating population size and trends throughout the region and designing and
101 implementing effective conservation measures.
102
103 Population assessments of marine turtles are routinely based on indirect counts, or estimates, notably track
104 counts, which in turn are used to estimate the number of nests per season, annual hatchling production, and/or

annual egg production (Schroeder & Murphy 1999; Frazier 2012). Although routinely used to estimate reproductive effort, female abundance, and population size, these estimators are based on several fundamental suppositions. Of particular importance are the assumptions that: (1) the proportion of the total number of tracks that are associated with successful nestings is relatively constant throughout a season, between seasons, and between females; (2) the mean number of successful nests per female per season remains relatively constant; and (3) the detectability of successful nests is reliable and consistent.

The present study documents nesting activity of green turtles for almost a decade at 5 contiguous beaches from South East Moheli, and assesses nesting seasonality and annual changes in abundance indicators, information that is fundamental for understanding population status and trends in order to help design effective conservation measures.

Materials and Methods

Study site and data collection

More than 1.6 km of beach on the east coast of Moheli (12° 18'S; 43° 35'E, Fig. 1) were monitored for this study. This area, immediately seaward and south of Itsamia village, is composed of five contiguous beaches which vary from less than 200 m to more than 500 m long: Itsamia beach (440 m), M'tsanga nyamba (510 m), Bwelamanga (160 m), Miangoni 1 (310 m) and Miangoni 2 (210 m) (Fig. 1). These beaches are separated from one another by narrow rocky promontories that are never more than 150 m wide, and they share similar topography and sand type. The nearest beaches to either side of the five Itsamia beaches where green turtles can nest are 1.5 km to the southwest, and 1.6 km to the northwest, although there is little evidence of nesting on either of these beaches. All five Itsamia beaches were monitored daily from the 1st of January 1999 until the 15th of June 2007 (8 years 5.5 months) for recording nesting attempts (tracks), and from 1st January 2000 to 31th December 2006 (7 years) for recording successful nestings (Table 1).

Track counts, routinely used to estimate nesting abundance (Schroeder & Murphy 1999) were calculated from empirical observations. Each time a female emerges from the water in an attempt to nest, she produces a set of tracks in the sand, one ascending the beach and the other descending back to the sea. By counting all the tracks on the beach, and dividing by two, it is possible to calculate the number of nesting attempts, or how much 'nesting activity' occurred on a particular beach since the last time tracks were counted (Godley et al. 2001). This number can provide an easily obtained indicator of nesting activity if tracks

are counted and marked daily, thus avoiding problems in track visibility from erosion by rain, wind, and/or high density nesting, as well as problems from double counting the same tracks.

In 1998, Kelonia and Ifremer staff trained two ADSEI members in basic field techniques, particularly for monitoring nesting beaches. Daily monitoring was carried out early in the morning by one or both ADSEI patrollers, and for an average of 4 months each year the ADSEI patrollers were assisted by an experienced staff member of either Kelonia or Ifremer. Patrols of the five beaches recorded the total number of nesting tracks (both ascending and descending); once recorded, each track was obliterated down to the intertidal zone to avoid re-counting on subsequent days.

As not all nesting attempts result in successful nestings (*i.e.* oviposition), it was necessary to evaluate spoor other than just the tracks, namely to check for signs of a filled in body pit with sand that had been thrown backwards as the female moved out of the cavity after depositing and covering eggs (Schroeder & Murphy 1999, Frazier 2012). Nonetheless, success at reading turtle nesting signs varies with the experience and skill of the observer; hence, the evaluation of successful nesting on the basis of reading spoor needs to be treated as an estimated parameter and further calculations based on this value must be undertaken with caution.

Missing data

Because it was not possible to monitor all five beaches each and every day over the eight and a half year period, there were occasional days when there was no patrolling effort. In order to avoid confusing past tracks from missed days, when the patrolling started again, patrollers only counted the last night's tracks, assessing track freshness based on signs of track erosion from wind, tide, and/or rain. We recognise that depending on the observer's experience, nesting density, and past weather conditions the track count for the last night can be either overestimated (by including tracks from more than the last night) or underestimated (by assigning some heavily eroded tracks from the last night to previous nights). We assumed in this study that these are random errors that will not affect the global trend and conclusions over the years.

Gaps in time series of nesting activity were interpolated following the method used Dalleau et al (2012), and the same dataset produced by Dalleau et al. (2012) was used in the present study.

Data management and simplification

A casual evaluation of the five adjacent Itsamia nesting beaches indicated no differences in seasonal trends or other nesting behaviour on individual beaches. Given that the five beaches are contiguous and of comparable

166 geophysical characteristics, but are clearly separated from other nesting beaches at Moheli, it was assumed that
167 these five beaches function as one "mega" beach. Hence, to reduce the complexity of the analyses, the five
168 adjacent Itsamia nesting beaches were treated functionally as one nesting beach. In addition, it was assumed that
169 the relationship between tracks and successful nestings that were made during nights with no monitoring was
170 comparable to the relationship from recorded data.
171
172 *Calculation of nesting indices*
173 The monitoring protocol allowed the calculation of a nesting success rate ($\hat{r}$) estimated as the ratio between the
174 total number of successful nestings observed and the total number of nest attempts (*i.e.* total number of tracks
175 divided by 2) observed during a nesting season (bearing in mind that both of these two values are minimal
176 because of missed nights patrolled): $\hat{r} = \frac{Successful\ nestings_{obs}}{Nest\ attempts_{obs}}$. Hence, the total number of successful
177 nests per season was estimated as the total number of nest attempts multiplied by the rate of nesting success $\hat{r}$;
178 total number of nest attempts in turn was estimated by including extrapolation of missing data using the method
179 of Dalleau et al. (2012). To estimate the total number of females nesting per season, we divided the total
180 number of successful nests per season by the average number of successful nestings per female per season ($\hat{m}$).
181 As there is no robust value of $\hat{m}$ for Itsamia beaches, we used the value from Saziley beach (Mayotte), an
182 intensively studied green turtle nesting beach similar to Itsamia beaches in structure and about 150 km from
183 Itsamia. The value $\hat{m}$ at Saziley was 3.03 (SD=0.37) (Bourjea et al. 2007a). The choice of this value is
184 discussed below.
185
186 *Data and trend analysis*
187 The trend in track counts of nesting green turtles at the Itsamia beaches was assessed using an additive model.
188 Monthly track counts time series from 1999 to 2006 was decomposed in smooth functions for the seasonal and
189 trend features in a Generalized Additive Mixed Model (GAMM), using the gamm function, of mgcv R-package
190 (Wood 2006). GAMM are semi-parametric Generalized Linear Models (GLM) where the linear predictor
191 depends on initially unknown smooth functions and takes into account the uncertainty induced by both random
192 effects and residual variability. A GAMM can be expressed as a combination between a Generalized Additive
193 Model (GAM) and a Linear Mixed Model (LME), the latter being exploited to fit the correlation structures in
194 the model residuals in order to account for the autocorrelation in the data. GAMM allow a flexible specification
195 of the link functions and error as well as the functional form of each predictor included in the regression model.

196 This method is widely used for the decomposition of complex time series (Bjorndal et al. 1999), and is
197 sometimes favoured to LOWESS smoothing methods (i.e. locally weighted scatterplots smoothing). For
198 comparison, classic seasonal decomposition of time series by Loess (STL, Cleveland 1990) was also applied to
199 our data set, yielding similar results to the GAMM analysis (see supplemental 1 for details).
200
201 The time series was decomposed into two smooth functions respectively applied to a x_1 covariate (i.e. the
202 month of the year) and a x_2 covariate (i.e. time elapsed since January 1999 in months). A random effect term
203 and a residual term also affected the response variable. Smooth functions for the seasonal covariate were set to a
204 cyclic smoothing spline of k=12 dimensions, whereas the trend covariate was wrapped in a cubic smoothing
205 spline. Considering the sample size and distribution, the model link function was set to an identity link, which is
206 the standard function for Gaussian distributions of the response data. Finally, an autoregressive seasonal effect
207 of order 1 (AR(1) nested within each year) was added to the model to account for residual. This model was
208 compared via a generalized likelihood ratio test (ANOVA) to a model containing only the seasonal component.
209 ANOVA was run on the LME model embedded within the GAMM procedure (see supplemental 2 for details).
210 Based on the result of the model, we estimated the increase of the average monthly number of nesting attempts
211 over the period by calculating the percentage of increase from the fitted value in 1999 and 2006.
212 All time series modeling procedures, regression analysis, and statistical tests used here were implemented using
213 the statistical analysis program R (R Core Team, 2013).
214

215 ## Results

216 *Monitoring, seasonality and nesting indices*

217 Over the 1999 – 2007 monitoring period, track counts were available for an average of 91.0% of the days of
218 each year (SD = 3.6%), varying from a minimum of 85.6% in 2000 to a maximum of 96.5% in 2004 (Table 1).
219 During these years there was no clear pattern for missing data, which were distributed over the entire data set. A
220 total of 153 682 nesting attempts were recorded, and when missing data were estimated, this corresponded to a
221 total of 169 138 estimated nesting attempts (8.5% increase in the total, Table 1). The daily time series of
222 estimated nesting attempts is shown in Fig. 2. This shows strong variation in the total number of nesting
223 attempts from year to year, a phenomenon that is usual and often documented in studies of green turtle nesting
224 (see review for the western Indian Ocean in Dalleau et al. 2012). Such variation could be due to environmental
225 stochasticity at foraging grounds and the relatively low position of the green turtle in the food-chain (Broderick
226 et al. 2001; Chaloupka et al. 2008). The median number of estimated nesting attempts per month for the

combined beaches from 1st January 1999 to 15th June 2007 shows a peak during the early austral winter from March through August (Fig. 3), with the highest average estimated values in May (2 265 nesting attempts, SD=994, n=9), and dropping during the period from November to February with the lowest in December, yielding an average of 993 nesting attempts for this month (SD = 679, n=8). Over all nesting success was estimated at $\hat{r}$=0.49 (SD=0.04; Table 1). Finally, for the seven-year period 2000 – 2006, a total of 63 164 successful nests was recorded, and when using the calculated rate of nesting success, there was an estimation of 69 630 successful nests during this period (Table 1).

Using the average number of successful nests per season per female from Saziley beach, Mayotte ($\hat{m}$=3.03), the average number of nesting females estimated for the five combined Itsamia beaches per season was 3 283 (SD = 1 760.8), with yearly averages that varied between a minimum of 924 females in 2000 to a maximum of 5 827 in 2005 (Table 1). The overall average number of nesters per season corresponds to a seasonal average of 2 014 nesters per kilometre of beach. However, these values are not meant to be taken as precise estimates, but rather as an order of magnitude. The large standard deviations observed for both average number nesting attempts per season and total number of nesting females per season are due to important increases in the number of nesting attempts from 2000 to 2006, as well as the large amout of yearly variation mentioned above (Table 1).

Long-term trend in nesting attempts

The GAM regression model (see supplement 2) embedded in the GAMM, including both trend and seasonal nonparametric smooth fits yielded an overall 0.66 adjusted-R^2 (Scale est. = 3.62e+05, n = 96), while trend and seasonal smooth terms were both significantly affected by the number of tracks per month (Seasonal smooth term: edf = 4.20, F = 4.29, p-value = 3.69e-07***; Trend smooth term: edf = 2.23, F = 6.07, p-value=0.003**). Trend over the time series for monthly nesting attempts was extracted. The fitted smooth of the predicted values using the trend component alone is shown in Fig. 4. This prediction of the trend contribution to the data was established under the assumption that seasonal and trend splines did not interact. Given the length of the study period, it was reasonable to assume that no significant change in the seasonal term had occurred over this time period. Confidence interval bands showed a widening towards extreme time values (Fig. 4). Indeed, estimates of the trend are less constrained at the end and beginning of the observation period, where less data are available. Using the fitted value of the model, we estimated that the number of nesting attempts increased 226% (391% - 143% based on fitted trend with 95% confidence intervals) from 1999 to 2006.

Discussion

Seasonality of nesting effort

Green turtles nest all year long at Moheli (Fig. 2 and Fig. 3); nonetheless, as at other nesting colonies, both regionally and worldwide (Bjorndal et al. 1999; Chaloupka 2001; Godley et al. 2001; Limpus et al. 2001, 2003; Bourjea et al. 2007a; Lauret-Stepler et al. 2007), they exhibit a distinct seasonal peak in nesting activity. The nesting peak at Moheli takes place during the austral winter, from March to August, which matches with the dry season at this island. A comparable pattern is documented for other nesting grounds in the region, such as Mayotte (Bourjea et al. 2007a), Grande Glorieuse (Lauret-Stepler et al. 2007), Aldabra atoll (Mortimer et al. 2012) and D'Arros island in the Amirantes (Mortimer et al. 2011b), as well as in Mozambique (Garnier et al. 2012).

Interestingly, Dalleau et al. (2012) demonstrated synchrony in nesting peaks between Moheli (Itsamia) and other rookeries in the northern part of the SWIO (*e.g.* Aldabra, Glorieuses, and Mayotte), but not with more eastern and southern rookeries (Tromelin and Europa). In fact, as shown by Lauret-Stepler et al. (2007) and Dalleau et al. (2012), not all nesting colonies in the SWIO exhibit the same seasonality; there is a clear peak in nesting during the wet season (austral summer) for Europa, in the south of the Mozambique Channel, and Tromelin, off the east coast of Madagascar. These marked differences in nesting seasonality are remarkable, for they occur over a relatively small geographic area and in populations that are thought to make breeding migrations of more than 1000 km in the SWIO (Hughes 1982; Le Gall & Hughes 1987). Thus, individual turtles may occur together in the same non-breeding areas, even though they have different seasonality of nesting. Nonetheless, oceanographic conditions, such as SST, are thought to have major impacts on on green turtle nesting seasonality in the SWIO (Dalleau et al. 2012).

Critical parameters in the nesting ecology of Moheli green turtles

The estimated average seasonal nesting success calculated from 2000 to 2006 varied from 0.40 to 0.52 over the study period, with a seven year average of 0.49 (SD=0.04; Table 1). Although records of successful nests were estimated from observations of turtle spore, and not direct confirmation of the presence of eggs, the annual values – with the exception of the first year - are remarkably similar. This indicates that these relatively constant estimates are reliable or that there is a constant error in the estimation, which is less probable. The seven-year average nesting success for Moheli is lower than the average value reported for some other nesting sites in the

289 SWIO, such as Mayotte 0.77 (SD=0.05; Bourjea et al. 2007a), Europa 0.66 (SD = 0.01; Le Gall 1988), and
290 Tromelin 0.56 (SD = 0.00; Le Gall 1988). It should be noted that these other nesting success estimations were
291 calculated from tagging and recapture that may overestimate this parameter by missing nesting turtles while
292 patrolling. Values for nesting success from outside the region estimated using tracks counts, can be either lower
293 than that for Moheli, such as 0.33 at Ascension Island (SD = 0.08; Godley et al. 2001) or higher such as 0.75 at
294 Vamizi, Mozambique (Garnier et al. 2012). Various environmental variables, such as density of nesters on the
295 beach, rain, tide, and condition of the subsurface sand may affect the success of nesting attempts (Limpus et al.
296 2003); physiological and behavioural conditions of the nesting females, as well as nesting experience, may also
297 affect nesting success (Perrault et al. 2012).
298 In order to estimate the number of nesting females using track counts, it is necessary to know the average
299 number of nests per season per female. The average value from Saziley beach Mayotte (3.03) was thought to be
300 the best estimate. Added to the fact that Mohéli and Mayotte are part of the same genetic stock (Bourjea et al.
301 2007b), the validity of this value is also supported by the fact that the mean number of nestings per female for
302 other islands in the SWIO region are comparable: Tromelin Island - with a single beach isolated on a remote
303 oceanic island, thus with highly reduced chances of immigration or emigration during the nesting season – was
304 somewhat higher ($\hat{m}$ = 3.50), and Europa Island was slightly lower ($\hat{m}$ = 2.80; Le Gall 1988). These values are
305 also similar to those from other sites in other regions, such as Ascension Island ($\hat{m}$ = 3.0; Mortimer & Carr,
306 1987), and Tortuguero, Costa Rica ($\hat{m}$ = 2.8; Carr et al. 1978).
307
308 *Trend in nesting attempts*
309 The increase from 1999 to 2006 (eight years) in the number of nesting attempts of 226% (391% – 143% based
310 on fitted trend with 95% confidence intervals) is remarkably high. However, this increasing trend does not
311 necessarily mean that the number of nesting females increased at this same rate; several things other than
312 population increase could explain this marked increase in nesting activity at the Itsamia beaches. An increase in
313 the number of nests per female would contribute to this trend. Additionally, a change in field techniques,
314 particularly the criteria for scoring a new track from old, or a change in scoring successful nestings, could
315 contribute to a perceived increase in successful nesting attempts (Schroeder & Murphy 1999); however, there is
316 no evidence for such a methodological change, for the ratio of successful to total nesting attempts remains
317 relatively stable after the first year (Table 1). Even if methods of estimating the increase in the number of
318 nesting attempts from one study to other one may change significantly, the annual increase in estimated number
319 of nesting females at Itsamia could be considered much greater than for other nesting sites in the SWIO

(Bourjea et al. 2007a, Lauret-Stepler et al. 2007). On Aldabra for instance, Mortimer et al. (2011a) estimated an increase of the annual number of nesters of 500 – 800% over 40 years. Outside the region, at major green turtle rookeries in the Atlantic and Pacific, population annual growth rates range between 0.038 and 0.139 (Chaloupka et al. 2008). These increases also correspond to sites were conservation measures were introduced and enforced for at least 25 years with the respective green turtle stocks recovering from serious depletion due to over-exploitation of eggs and turtles (Ehrhart & Bagley 1999; Chaloupka & Limpus 2001; Balazs & Chaloupka 2004; Troëng & Rankin 2005; Chaloupka et al. 2008).

Why such an important increase at Itsamia?

Several factors may be involved. First, it's important to note that the number of years of data available for the trend analysis at Itsamia was 8 years, whereas 20 and 23 years' of data were available respectively for Europa and Tromelin (Lauret-Stepler et al. 2007); and for Rain island 31years of data were analysed (Chaloupka et al. 2008). The Rain island study showed a higher increase for the first 10 years of monitoring, followed by a lower rate of increase in subsequent years – this deceleration in the rate can be expected for Itsamia.

The recent history of turtle exploitation at the Itsamia beaches may also be relevant. Until 1980 these beaches were relatively isolated, and accessible primarily to the people of Itsamia village. Because of religious beliefs these people did not, and do not, eat or kill marine turtles. In 1972 the Itsamia beaches were found to have the largest concentration of nesting green turtles in Moheli, or all of Comores (Frazier 1985), indicating that turtles had not been exploited on these beaches for many decades. In 1983 a bilateral aid programme with Japan resulted in small, motorised fishing boats (called Japawas) becoming available in Comoros. As a result, fishermen from Anjouan and Grande Comore could travel relatively quickly and easily to the coast of Moheli, allowing them to exploit nesting green turtles from the Itsamia beaches. As many as 10 to 30 nesters were caught per day, and this continued until 1991 when the Itsamia villagers decided to deny access to fishermen from Anjouan and Grande Comore to Itsamia beaches (M'Soili, pers. obs.). Since that date, there have been only a few reports of turtle poaching from these beaches (M'Soili, pers. obs.). Hence, after an extended period of low, or no, exploitation, Itsamia beaches were subjected to intense exploitation from 1983 to 1991. Since green turtles require at least 25 to 30 years to reach sexual maturity (Limpus & Walter 1980), even during the period of intense exploitation at Itsamia, there should have been significant recruitment into the nesting population from nesting that had occurred before 1983. Hence, once intense exploitation was stopped in 1991 the nesting population, which is comprised of both new recruits and returning nesters, would have been expected to grow relatively rapidly.

Immigration of nesting females that might otherwise have nested at other beaches around Itsamia, or elsewhere in the Comores or the region, could also contribute to an increase in the number of nesting females at the Itsamia beaches. Increased immigration of nesting females to Itsamia, with an increase in numbers at this important rookery could occur, although the population size of the management unit may not experience an increase. As the Itsamia beaches and offshore waters now enjoy protection while other nearby nesting sites on Moheli and other beaches in Comores are subject to continuing perturbation, reproductive turtles could be driven out of the disturbed areas to the safer Itsamia beaches. An increase in the number of nests per female per season, could result in a significant increase in annual nesting activity; this could be tied to maturational changes with increased fecundity and/or enhanced forage conditions with improved reproductive output (Limpus & Chaloupka 1997).

However, the dataset used in the analysis stops at 2007. The question that remains is: what is the situation in 2014? We know that the nesting activity is still very high (M'soili pers.obs.), but the available observations do not allow objective comparisons with the datasets used in this study, and it is almost impossible to estimate if the annual increase in nesting attempts is still the same or if it slowed down.

Regional importance of Itsamia nesting beaches

With the results of the present study, there are now reliable estimates of the number of nesting green turtles per season for several important rookeries in the SWIO. Europa Island hosts the largest colony with between 3 000 and 10 000 green turtles nesting per season (Le Gall et al. 1988); Aldabra is next with 3100 to 5225 (Mortimer et al. 2011a); Mayotte has more than 2000 nesters on just the two most important nesting sites (Bourjea et al. 2007a); Tromelin has between 1000 and 3 000 (Le Gall et al. 1988), and Grande Glorieuse had some 1 480 nesting females on just 26% of the suitable nesting sites (Lauret-Stepler et al. 2007). Just the five Itsamia beaches of Moheli clearly provide a significant component to the total number of nesters in the region, with more than 5000 nesters per season estimated. Considering scores of other nesting beaches on Moheli, particularly the islands off the southern coast (Frazier 1985; Beudard pers. obs.), the total nesting population at Moheli is be one the largest in the SWIO; it could be second only to Europa. Including other nesting sites in the Republic of Seychelles (particularly Cosmoledo Atoll, and the Amirantes Islands; Mortimer et al. 2011b), Mozambique (Bazaruto, Primeiras and Segundas, Garnier et al. 2012), the East Africa (Tanzania and Kenya, Frazier 1984), Iranja Kely island in Madagascar (Bourjea et al. 2006), it is clear that the SWIO is one of the most important regions in the world for green turtles.

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Tables and Figures

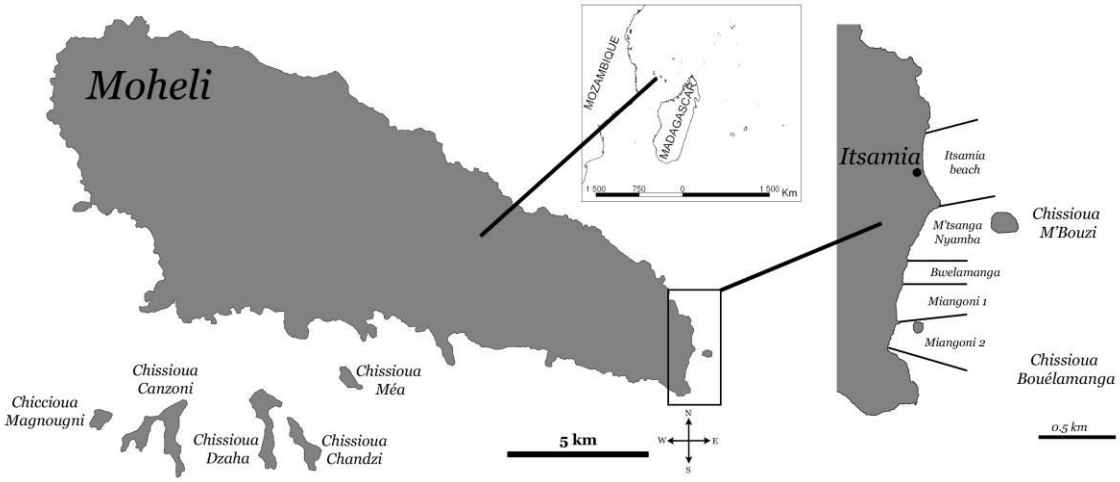
Fig. 1 : Moheli (12° 18'S; 43° 35'E), smallest of the 4 main islands of the Comoro Archipelago, showing the five contiguous beaches (Itsamia beach, M'tsanga nyamba, Bwelamanga, Miangoni 1 and Miangoni 2) that were monitored for tracks (January 1999 to June 2007) and successful nests (January 2000 to December 2006)

Fig. 2 : Monthly time series of female green turtle tracks recorded on Itsamia beaches, Moheli (January 1999 – June 2007) after interpolation of missing values on daily time series

Fig. 3 : Box and whisker plot of the monthly average number of estimated nesting attempts (tracks) on the five contiguous Itsamia beaches, Moheli, Comoro Archipelago, over the period from January 1999 through June 2010, based on daily monitoring. Thick horizontal line in each box: 50th percentile (median) of number of tracks for each month; upper and lower boundaries of each box: 75th and 25th percentiles, respectively; top and bottom of the whiskers: 90th and 10th percentiles, respectively; plots above the 90th percentile: extreme outliers

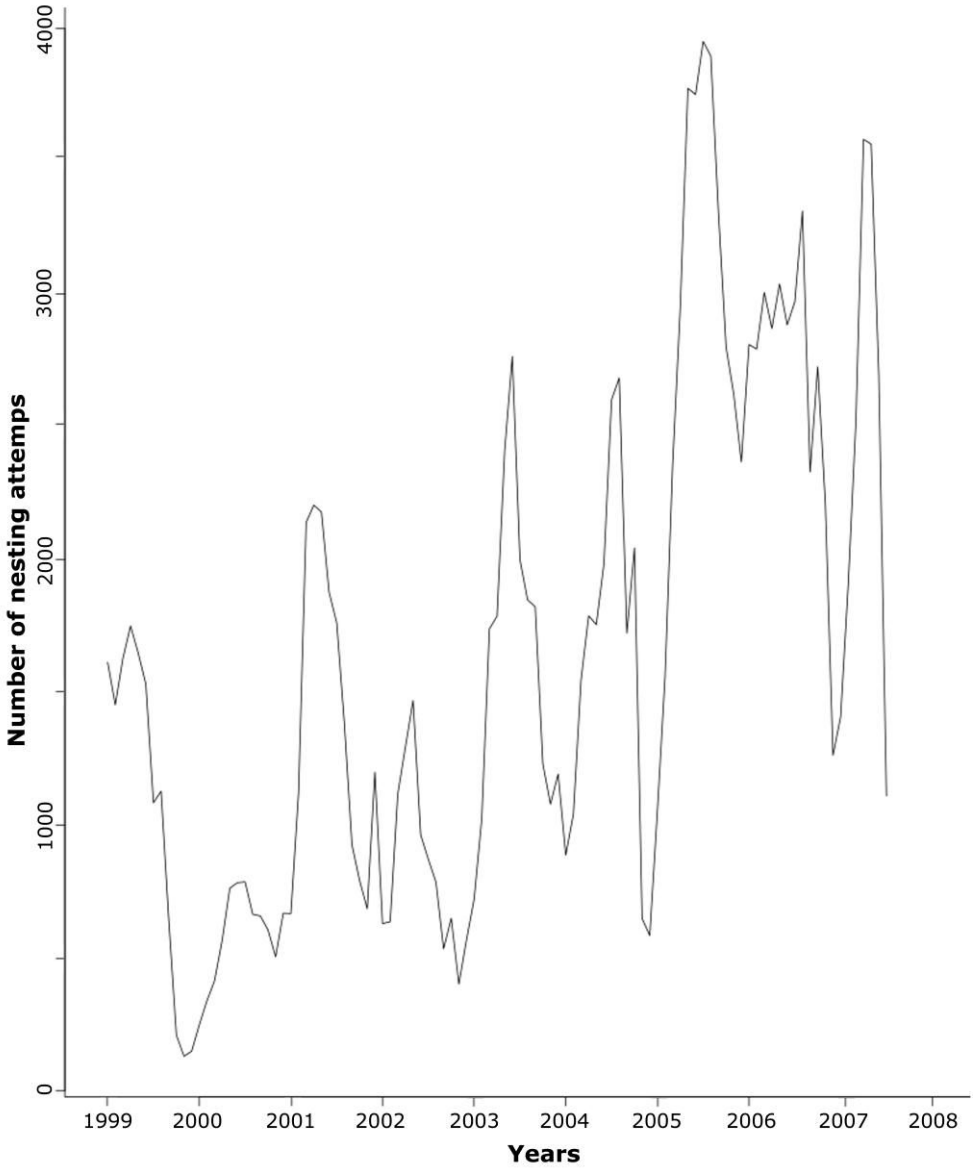
Fig. 4 : Fitted Trend component in Itsamia beaches monthly track counts from 1999 to 2007, Moheli, Comoros Archipelago. Solid line is the fitted smooth (cubic smoothing spline) of the predicted number of tracks per month from the GAMM trend component; dashed lines are 95% confidence intervals; grey open circles are observed track counts; dotted line is the linear regression slope calculated on Gam fitted values (R^2=0.88, df = 94, slope coefficient=17.7 SE 0.7)

517 **Fig. 1**



518

519 **Fig. 2**



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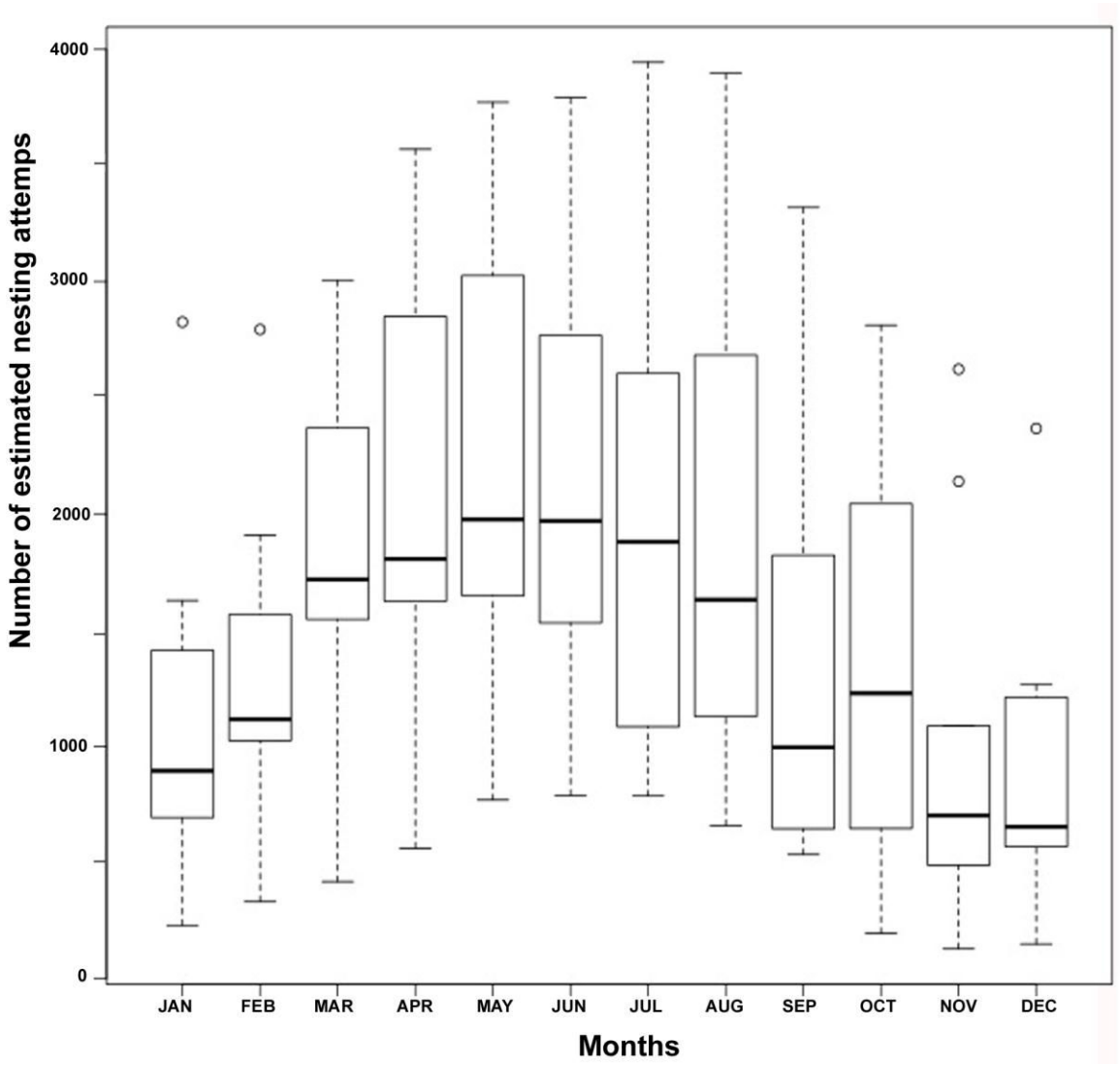
521 **Fig. 3**



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524 **Fig. 4**

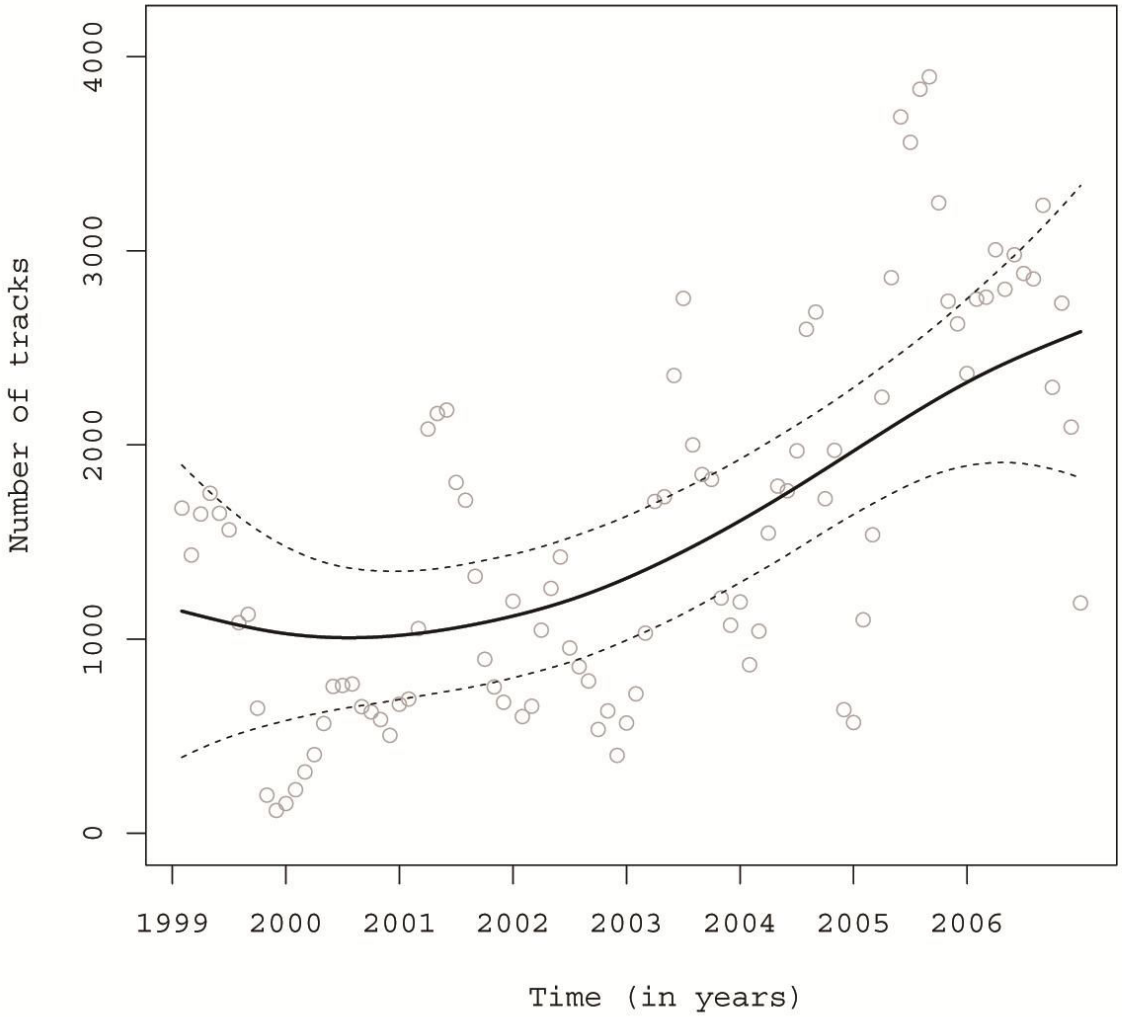

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Table 1 : Summary of beach monitoring results from 1st January 1999 through 15th June 2007 on the five contiguous beaches, Itsamia, Moheli, Comoro Archipelago; yearly and average values for five contiguous Itsamia beaches combined (Itsamia beach, M'tsanga nyamba, Bwelamanga, Miangoni 1 and Miangoni 2): estimated values were calculated by correcting for missing data by extrapolating (see Material and Method section); Nest attempts: sum of tracks/2 for all days that had beach patrols; Successful nestings: sum of nest attempts that had signs of successful nesting, for all days that had beach patrols; Total estimated number of nest attempts: sum of estimated nest attempts per month for all of the days of the months; $\hat{r}$ **= nesting success calculated as follows:** $\hat{r} = \frac{Successful\ nestings_{obs}}{Nest\ attempts_{obs}}$ **;** $\hat{m}$ **= 3.03 is the average number of successful nests per female per season calculated for Mayotte (Bourjea et al. 2007a); the total number of turtles nesting per season was estimated by dividing the total number of successful nests estimated per season by** $\hat{m}$ **; SD = Standard Deviation.**

Year	Sampling period	Number of months	Nest attempts	Successful nestings	Effort (% of days)	$\hat{r}$	Total estimated number of nest attempts	Total estimated number of successful nestings	Number of turtles (m=3,03)
1999	**all year**	12	12379	-	93.6	-	12996	-	
2000	**all year**	12	5977	2398	85.6	0.40	6982	2801	924
2001	**all year**	12	14547	7184	86.5	0.49	16977	8384	2767
2002	**all year**	12	8688	4390	90.5	0.51	9890	4997	1649
2003	**all year**	12	18449	9536	95.1	0.52	19691	10178	3359
2004	**all year**	12	18635	9574	96.5	0.51	19260	9895	3266
2005	**all year**	12	30924	15818	90.4	0.51	34514	17654	5827
2006	**all year**	12	29087	14264	91.0	0.49	32057	15720	5188
2007	**1th January - 15th June**	6	14996	-	89.8	-	16771	-	-
TOTAL		**102**	**153682**	**63164**	**91.0**		**169138**	**69630**	
				Average	**91.0**	**0.49**		**9947.2**	**3283**
				SD	**3.6**	**0.04**		**5335.4**	**1760.8**

CHAPITRE 1 – SYNTHESE : CONNAITRE L'ABONDANCE EN REPRODUCTEURS ET LA TENDANCE EVOLUTIVE

Ce dernier siècle a vu les populations de nombreuses espèces de grands animaux emblématiques s'effondrer face à la dégradation des habitats et aux menaces anthropiques qui pèsent sur elles (Malakoff, 1997). La conservation de ces espèces à large répartition spatiale, longévives et à maturité sexuelle tardive passe avant toute chose par une bonne évaluation de l'échelle écologique à laquelle seront appliquées les mesures de conservation et surtout leur ordre de priorité. Dans le cas des tortues marines qui ont subi des siècles d'exploitation de par le monde (Parsons, 1962) et dans l'océan Indien en particulier (Frazier 1980), l'une des priorités de gestion est une vision claire de l'abondance des individus reproducteurs pour une population identifiée ainsi que de son évolution dans le temps.

Les travaux menés dans le cadre de cette thèse ont permis de contribuer dans un premier temps à un meilleur état des lieux du nombre de femelles de tortues vertes en reproduction dans l'océan Indien occidental (voir synthèse Fig. 1.1). On y retrouve par exemple des sites de pontes parmi les plus importants au monde, comme Europa (7 – 10 000 femelles en reproduction; Le Gall, 1988); Aldabra (~6 000 femelles, 17 – 18 000 nids ; Mortimer et al., 2011b), Mayotte (~3500 femelles; Bourjea et al., 2007 – Chapitre 1, section 1), Mohéli (~4000 – 6000 femelles; voir Chapitre 1, section 2) et Tromelin (~1000 individus; Le Gall, 1988); la Grande Glorieuse (1 480 femelles en ponte sur 26% des plages exploitables (Lauret-Stepler et al., 2007; ceci permet d'estimer, en considérant que la zone suivie est de loin la plus productive de l'île, qu'environ 3 à 4 000 tortues vertes viennent pondre tous les ans (Base de données TORSOOI – www.torsooi.com), ou encore Cosmoledo (~1000 – 5000 nids; Mortimer et al., 2011b, soit ~250 – 1000 femelles).

Il est important de noter que cette région abrite également de nombreux sites de reproduction situés sur des îles isolées et qui, tout en restant modestes quant au nombre de reproducteurs qu'ils accueillent, n'en contribuent pas moins très probablement à la dynamique régionale de cette espèce (Fig.1.1). On y retrouve notamment l'ensemble des îles Granitiques Seychelloises (<200 nids; Mortimer, 1984; Bird Island Lodge and North Island Seychelles données non publiées; soit <50 femelles), du groupe des Amirantes (<750 individus, <3500 nids; Mortimer et al., 2011a, J.A. Mortimer et Island Conservation Society, données non publiées), du groupe Farquhar (<500 individus; Mortimer, 1984), Juan de Nova (10 – 30 individus; Lauret-Stepler et al., 2010). On retrouve par contre beaucoup plus rarement de nos jours des individus en reproduction dans l'archipel des Mascareignes comme à La Réunion (~1-2 femelles ; Ciccione et Bourjea, 2006).

On retrouve également des sites peu productifs le long des côtes continentales comme à Madagascar (e.g. Nosy Iranja Kelly, 100 – 150 nids; Bourjea et al., 2006; soit <50 femelles), cette île-continent qui pourrait voir tous les ans au total de nombreuses tortues vertes se reproduire sur les côtes nord, ouest et sud si le braconnage n'y était pas intense (Rakotonirina, 2012); ou encore le long de la côte est africaine comme en Tanzanie (île de Mafia et alentour, 250 – 300

nids; Muir, 2005; soit < 80 femelles), au Kenya (Okemwa et al., 2004) ou encore au Mozambique comme sur l'île de Vamizi sur l'archipel des Quirimbas (100 – 150 nids; Garnier et al., 2012; soit <50 femelles), à Bazaruto ou sur l'archipel Primeira et Segunda (Videira et al., 2011).

Mais un manque d'informations persiste sur la réalité des sites de ponte qui ont par le passé été recensés comme potentiellement intéressants (Hughes 1973; Frazier 1975; 1982). En effet, les données disponibles aujourd'hui ne permettent pas d'en évaluer l'intérêt et des évaluations quantitatives, ou *a minima* qualitatives, devraient être mises en place en priorité dans le cadre d'une réflexion régionale de conservation de ces espèces, telle celle menée par l'IOSEA MoU (Indian Ocean and South East Asia Memorandum of Understanding for the Conservation of Marine Turtle and their Habitat). C'est le cas notamment des sites comme Agalega, Saint Brandon, les Chagos – Maurice ou encore le long de la côte somalienne, une zone déjà connue pour être un site d'alimentation non négligeable pour les tortues vertes se reproduisant dans les îles du sud-ouest de l'océan Indien (Bourjea et al., 2013; Dalleau, 2013) et qui très certainement abritent des sites de reproduction qui restent à évaluer.

Dans un second temps, et lorsque les données le permettaient, ce travail a contribué à évaluer la tendance d'un indice d'abondance de femelles se reproduisant sur certains sites de reproduction du sud-ouest de l'océan Indien. Ces évaluations, exploitant des données acquises sur le long terme, sont une étape indispensable pour estimer l'état de conservation d'espèces longévives à maturité sexuelle tardive et dont les traits de vie sont aussi complexes que ceux des tortues marines (Musick, 1999). Les résultats ont permis de mettre en évidence que pour les principaux sites de reproduction des tortues vertes de cette région, le nombre de reproducteurs est stable ou croissant depuis ces 10 à 20 dernières années (Lauret-Stpeler et al., 2007; Bourjea et al., 2007; Mortimer et al., 2011b; Bourjea et al., 2011), signe que les programmes et mesures de conservation ont été efficaces sur ces sites.

Cependant, si ces évaluations ont été possibles grâce au suivi d'indicateurs de la reproduction sur des sites comme les îles Eparses (e.g. Europa depuis 1983, les îles coralliennes seychelloises (e.g. Aldabra depuis 1980) ou les îles de l'archipel des Comores plus récemment (e.g. Mayotte et Mohéli depuis 1998; Chapitre 1, section 1,2), il n'en reste pas moins que trois points majeurs doivent être pris en considération dans les années à venir.

Le premier est la nécessité de réévaluer les paramètres biologiques liés à l'activité de ponte des reproducteurs site par site. En effet, les indicateurs de l'abondance de reproducteurs utilisés pour faire ces évaluations sont généralement le nombre de traces laissées lors de l'émergence sur la plage pour pondre, ou le nombre de traces de nids laissées par la ponte. En aucun cas, ils ne représentent la réalité de l'évolution du nombre de reproducteurs. Ainsi, une augmentation du nombre de traces par exemple peut soit refléter une augmentation du nombre d'individus montant sur la plage pour pondre, soit une augmentation du nombre d'échecs à la ponte, impliquant des montées successives pour une seule ponte. L'indicateur peut donc être facilement biaisé par des changements du comportement reproductif dans le temps. Ces modifications sont généralement liées soit à i) des changements physiologiques (i.e. le rajeunissement ou le vieillissement) de la population, ii) des variations de conditions

environnementales (i.e. une dégradation de l'habitat rendant plus difficile l'acte de ponte) ou iii) des perturbations anthropiques récurrentes (e.g. la fréquentation touristique sur une plage). L'acquisition en routine de ces indicateurs de l'abondance d'une population doit donc impérativement être accompagnée, de manière périodique (tous les 5 ans semble être un compromis coût/résultats intéressant) d'une réévaluation des paramètres reproductifs des tortues marines.

Le second, et qui doit être mené en parallèle avec la réévaluation des paramètres reproductifs, est le suivi de la production en nouveau-nés. En effet, de la même manière que pour l'indicateur «trace», un même nombre de traces d'une année à l'autre peut amener à des productions de nouveau-nés complètement différentes. Un déclin de la production de nouveau-nés peu en effet avoir un impact sur la population à long terme significatif comme par exemple la chute des recrutements de nouveaux reproducteurs dans la population. Une telle chute pourrait alors être attribuée à des prélèvements massifs dans la population de reproducteurs (e.g. capture accidentelle), alors qu'il est dans les faits liés à la dégradation de la production de nouveau-nés. L'objectif est donc d'évaluer périodiquement cette production de nouveau-nés afin de s'assurer de la productivité d'une population dans le temps. Par exemple, cette réévaluation par un suivi terrain intense de la reproduction des tortues vertes vient d'être réalisée pour Tromelin, avec une analyse comparative des paramètres reproducteurs estimés sur la période 1973-1983 et 2009-2010 (Derville et al., soumis). Les résultats ont montré que les paramètres reproductifs et de production de nouveau-nés des tortues vertes se reproduisant à Tromelin étaient particulièrement stables dans le temps et donc que les évaluations d'abondance étaient faiblement biaisées par les variations intrinsèques de la reproduction.

Enfin, dans un contexte de changement climatique, la disponibilité de jeux de données journaliers fiables sur le long terme est un enjeu majeur. Des travaux récents exploitant ces séries longues ont permis par exemple de mettre en évidence le rôle structurant de la température dans la phénologie de la reproduction des tortues vertes dans le sud-ouest de l'océan Indien (Dalleau et al., 2012) et de mieux appréhender les conséquences d'une augmentation de la température de surface de l'eau sur la saisonnalité de la reproduction dans cette région du monde, une saisonnalité marquée par des différences très importantes sur de faibles distances (Lauret-Stepler et al., 2007). Au-delà du suivi des adultes, assurer le suivi de la production de nouveau-nés doit être considéré comme une priorité pour bien évaluer les conséquences d'une augmentation de température non seulement sur la saisonnalité, mais aussi sur la production et la détermination épigénétique du sexe des nouveau-nés. En effet, la température a un rôle majeure dans le sexe ratio des reptiles, avec par exemple chez la tortue verte une température pivot de 29,5°C au-delà de laquelle les femelles seront favorisées (Godfrey et Mrosovsky, 2006).

Le suivi de la reproduction est donc un des piliers de la conservation de la mégafaune. Il permet d'appréhender les caractéristiques d'une population de tortues marines à l'échelle d'un site de reproduction lors d'une phase clé de leur cycle biologique et de déceler des menaces qu'elle pourrait être en train de subir. Par contre, ce suivi seul ne peut permettre d'avoir une vision de l'ensemble du système, et d'autres informations sont nécessaires pour comprendre (i) les

relations qu'il existe entre les individus de cette population, (ii) les différents espaces qu'ils occupent aux différentes phases de leur cycle de vie et (iii) les relations que ces individus peuvent avoir, ou pas, avec des individus originaires de sites voisins. Si l'approche par l'écologie spatiale est certainement l'une des approches les plus performantes actuellement pour comprendre la dynamique spatiale de ces populations à l'échelle régionale, ce sujet a déjà fait l'objet d'un travail intense et ne sera pas développé ici (Dalleau, 2013).

Par contre l'approche par la génétique des populations peut se révéler très performante car elle permet d'avoir une vision régionale, d'évaluer la dispersion de ces populations et de définir leurs limites spatiales (Palumbi, 2003). Cette approche s'est montrée particulièrement efficace dans le cas de tortues marines dans d'autres océans pour établir la structure des stocks et leur connectivité (Avise, 1998; Bowen et Karl, 2007). La détermination de cette structure spatiale est l'objectif du Chapitre 2.

Fig.1.1 : Etat actuel des connaissances sur le nombre estimé de femelles de tortues vertes *Chelonia mydas* se reproduisant par an sur les sites de ponte de l'océan Indien Occidental (source: voir Chapitre 1; Base de données TORSOOI, Kelonia, Ifremer, Natural Earth, GADM, Marine Region; Sextant Océan Indien, PNA Tortue marine Océan Indien, Volet Régional)

CHAPITRE 2 – Identifier la structure génétique d'une espèce pour optimiser sa gestion régionale

Ce chapitre est décomposé en 2 sections et une synthèse.

La section 1 est constituée d'un article présent ant pour la première fois la structure génétique régionale des tortues vertes femelles se reproduisant dans le sud-ouest de l'océan Indien.

Bourjea, J., Lapègue, S., Gagnevin, L., Broderick, D., Mortimer, J.A., Ciccione, S., Roos, D., Taquet, C., Grizel, H., 2007. Using mtDNA sequences in the phylogeography of the green turtle, Chelonia mydas, in the south west Indian ocean. Molecular Ecology 16, 175–18.

La section 2 est constituée d'un article soumis présentant une révision de cette structure génétique obtenue grâce à de nouveaux sites de ponte échantillonnés aux Seychelles et en Afrique de l'est, ainsi que par les résultats de suivis par satellites de tortues depuis les Seychelles.

Bourjea, J., Mortimer, J.A., Garnier, J., Okemwa, G., Godley, B., Hughes, G., Dalleau, M., Jean, C., Ciccione S., Muths, D., submitted. Population structure enhances perspectives on regional management of the western Indian Ocean green turtle. Conservation Biology.

La synthèse présente un bilan de la structure génétique des tortues vertes femelles en reproduction dans le sud-ouest de l'océan indien et discute de l'état de conservation de la diversité génétique de cette espèce. Cette synthèse propose aussi de nouvelles approches en biologie moléculaire qui pourraient permettre de mieux répondre aux problématiques de conservation régionale de la mégafaune marine.

CHAPITRE 2 – SECTION 1 : PHYLOGEOGRAPHIE DE LA TORTUE VERTE, CHELONIA MYDAS, *DANS LE SUD-OUEST DE L'OCEAN INDIEN*

PHYLOGEOGRAPHY OF THE GREEN TURTLE, *CHELONIA MYDAS*, IN THE SOUTHWEST INDIAN OCEAN

Auteurs : Bourjea, J., Lapègue, S., Gagnevin, L., Broderick, D., Mortimer, J.A., Ciccione, S., Roos, D., Taquet, C., Grizel, H.

Année : 2007

Journal: Molecular Ecology

Numéro: 16

Pages: 175–18

A retenir :

- Exploration de la phylogéographie de la tortue verte femelle en reproduction dans le sud-ouest de l'océan Indien
- Analyse des variations de l'ADN mitochondrial de 288 échantillons collectés sur 10 sites de reproduction différents
- Mise en évidence d'un flux de gènes récent de l'Atlantique vers l'océan Indien via le Cap de Bonne Espérance
- Identification de deux unités de gestion génétiques différentes, l'une dans le sud du Canal du Mozambique (SMC), et l'autre dans le nord (NMC)
- L'Unité SMC pourrait être subdivisée en 2 sous-unités
- Cette structuration génétique est très probablement due aux caractéristiques océanographiques rencontrées dans le sud-ouest de l'océan Indien, et plus particulièrement dans le canal du Mozambique.

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Phylogeography of the green turtle, *Chelonia mydas*, in the Southwest Indian Ocean

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Abstract

Patterns of mitochondrial DNA (mtDNA) variation were used to analyse the population genetic structure of southwestern Indian Ocean green turtle (*Chelonia mydas*) populations. Analysis of sequence variation over 396 bp of the mtDNA control region revealed seven haplotypes among 288 individuals from 10 nesting sites in the Southwest Indian Ocean. This is the first time that Atlantic Ocean haplotypes have been recorded among any Indo-Pacific nesting populations. Previous studies indicated that the Cape of Good Hope was a major biogeographical barrier between the Atlantic and Indian Oceans because evidence for gene flow in the last 1.5 million years has yet to emerge. This study, by sampling localities adjacent to this barrier, demonstrates that recent gene flow has occurred from the Atlantic Ocean into the Indian Ocean via the Cape of Good Hope. We also found compelling genetic evidence that green turtles nesting at the rookeries of the South Mozambique Channel (SMC) and those nesting in the North Mozambique Channel (NMC) belong to separate genetic stocks. Furthermore, the SMC could be subdivided in two different genetic stocks, one in Europa and the other one in Juan de Nova. We suggest that this particular genetic pattern along the Mozambique Channel is attributable to a recent colonization from the Atlantic Ocean and is maintained by oceanic conditions in the northern and southern Mozambique Channel that influence early stages in the green turtle life cycle.

Keywords: *Chelonia mydas*, control region, Indian Ocean, mitochondrial DNA, Mozambique Channel, phylogeography

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Introduction

The green turtle (*Chelonia mydas*) is a large, long-lived, herbivorous reptile that grazes on marine macrophytes in shallow tropical and subtropical waters around the world (Limpus *et al*. 1994; Limpus & Chaloupka 1997). Because green turtle hatchlings are rarely seen between the time they leave their natal beach and when they first appear in shallow water foraging habitats (Musick & Limpus 1997), Carr (1987) named this interval the 'lost year'. Available evidence now indicates that this lost year involves at least several years of drifting in oceanic gyre systems in a passive migration that may circumnavigate entire ocean basins (Bowen *et al*. 1995; Bolten *et al*. 1998; Lahanas *et al*. 1998). Green turtles grow slowly, often taking some 25–30 or more years to reach maturity (Limpus & Walter 1980). During this developmental period, they occupy a series of foraging habitats dispersed over an extensive area. Upon

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reaching adulthood, reproductive females typically make long distance migrations between feeding sites and their natal breeding beaches (Limpus *et al*. 1992). They show great fidelity to both nesting (Meylan 1982) and feeding grounds (Limpus *et al*. 1992), even though these may be separated by thousands of kilometres (Mortimer & Carr 1987). They typically lay multiple clutches within a season (Carr & Ogren 1960), with 1–9 or more years separating successive breeding seasons (Le Gall *et al*. 1985; Limpus *et al*. 1994, 2001; Miller 1997).

Attempts have been made to define green turtle population boundaries for this globally distributed endangered species in order to identify functional units of management. Although flipper tagging (Le Gall & Hugues 1987), satellite (Pelletier *et al*. 2003) and acoustic telemetry (Taquet *et al*. 2006) provide useful information about contemporary demography, site fidelity and migrations of individual animals, the data produced are strongly biased towards females and intensively surveyed locations, especially nesting beaches. In contrast, genetic studies tend to focus on the population rather than on the individual level that can offer unique perspectives on historical population dynamics. When complemented by tagging studies, genetic tools can elucidate the geographical boundaries of breeding populations and provide information about their migrations through feeding, breeding and developmental ranges (Bowen & Karl 1997).

Mitochondrial DNA (mtDNA) has proven particularly effective for detecting population structure in marine turtles (FitzSimmons *et al*. 1999), and several studies have successfully used mtDNA variants to resolve population boundaries among breeding sea turtles (Bowen *et al*. 1992, 1994, 1998; Broderick *et al*. 1994; Norman *et al*. 1994; Bass *et al*. 1996; Encalada *et al*. 1996; Dutton *et al*. 1999). In general, these studies have revealed a significant level of population subdivision on both regional and global scales and found that rookeries, often separated by hundreds of kilometres, may form genetically discrete populations or management units (Moritz 1994). The maternal inheritance of mtDNA also tends to accentuate genetic differences among populations compared to nuclear genes because it has a smaller effective population size. In many circumstances, female-inherited markers offer a distinct advantage because they provide perspectives on female reproductive behaviour that are paramount to species survival (FitzSimmons *et al*. 1999). Nevertheless, mtDNA does not capture the entire population genetic history of a particular species and inferences of population connectivity and isolation can be misleading especially if male–mediated gene flow is substantially different to that of females, as it was shown in some green turtle populations (Karl *et al*. 1992; FitzSimmons *et al*. 1997a, b, 1999; Roberts *et al*. 2004).

Among the significant green turtle rookeries that occur in the Southwest Indian Ocean, some have been well described. At the French Eparses Islands (Europa, Juan de Nova, Tromelin and Glorieuses), green turtle populations have been monitored since the 1980s (Le Gall *et al*. 1985; Le Gall & Hugues 1987; Le Gall 1988). The green turtles of the Seychelles archipelago are well known (Frazier 1984; Mortimer 1984; Mortimer *et al*. in press), especially those at Aldabra (Frazier 1971; Mortimer 1988). Other studies include those of green turtles at Mayotte (S. Ciccione, unpublished data), Comoros (Frazier 1984; S. Ciccione, unpublished data), Northeast of Madagascar (J. Bourjea, unpublished data), Kenya (Okemwa *et al*. 2004), and Tanzania (Muir 2005). These studies have shown that the patterns of movements and behaviour of green turtles in this region conform to those found elsewhere in the world, but a detailed appraisal of the entire region has yet to emerge. In fact, information on nesting turtles is either sparse or lacking in other adjacent countries, especially Mozambique, South of Madagascar and Somalia, where both nesting and foraging habitat as well as human exploitation of this species occur (Le Gall & Hugues 1987; Rakotonirina & Cooke 1994).

The Southwest Indian Ocean, especially the Mozambique Channel, is of particular biogeographical interest. Suitable green turtle feeding habitat, due to warm water flows, are found very close to the tip of South Africa while suitable habitat is absent from the west coast of South Africa due to upwelling and cold water flows. Previous protein and total mtDNA restriction fragment length polymorphism (RFLP) genetic studies inferred that cold waters of South Africa have been a major biogeographical barrier for green turtle dispersal (Bonhomme *et al*. 1987; Bowen *et al*. 1992). Bowen *et al*. (1992) found no evidence of gene flow occurring between Indian and Atlantic Oceans over the last 1.5 million years but they did not sample rookeries in the Mozambique Channel. If there is any contact between green turtles in the Indian and Atlantic Oceans, then the Mozambique Channel is the most likely place for this to occur.

The purpose of this study is to survey the patterns of mtDNA control region sequence variation of nesting green turtles at 10 different rookeries in the Southwest Indian Ocean, principally along the Mozambique Channel. The patterns of mtDNA variation will be used to: (i) define groups of rookeries that comprise discrete genetic populations; (ii) investigate the patterns of dispersal and subdivision of rookeries in this region; and (iii) determine if there is any evidence of contact between green turtles from Indian and Atlantic Oceans.

Materials and methods

Sampling

A total of 288 nesting females were sampled on different dates from 10 different nesting sites in the western Indian

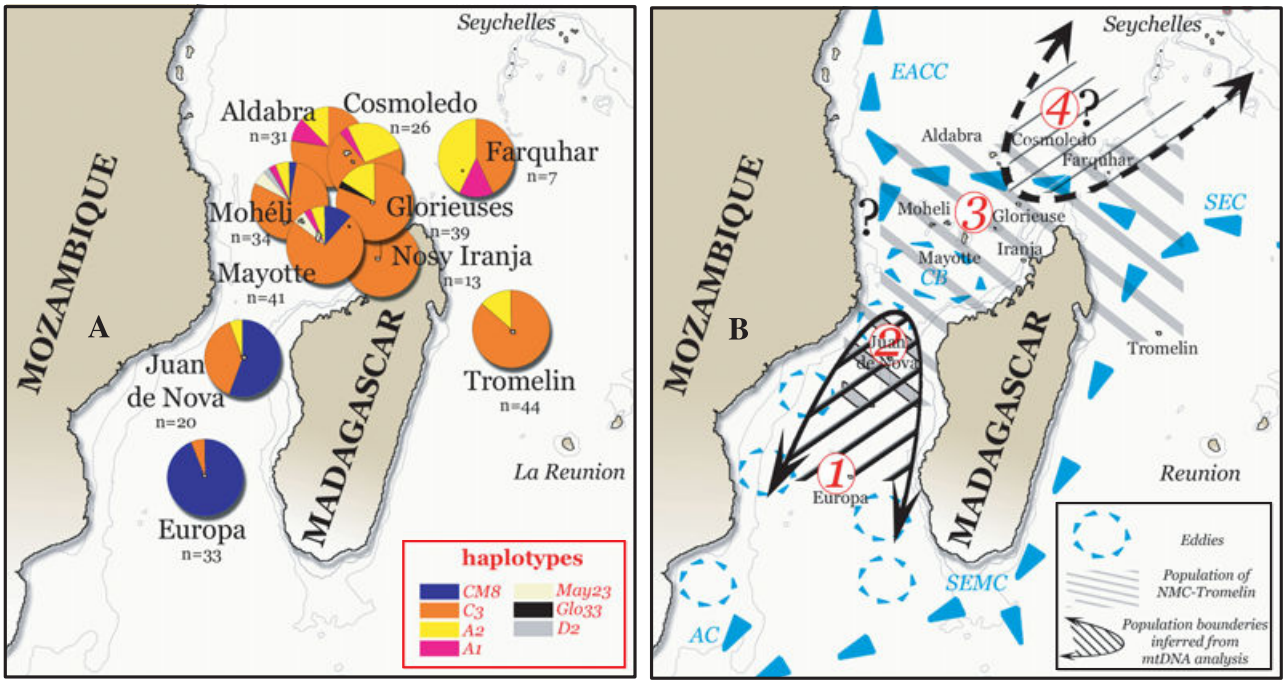

Fig. 1 (A) Geographical locations of the 10 green turtle nesting sites sampled in the Southwest Indian Ocean. The piechart shows the frequencies of the haplotypes per nesting site. (B) Main oceanic movements in the Southwest Indian Ocean and nesting green turtle population boundaries inferred from mtDNA data. The following abbreviations were used: SEC, South Equatorial Current; SEMC, Southeast Madagascar Current; EACC, East African Coastal Current; AC, Agulhas Current; CB, Comoro Basin. The numbers (1, 2, 3, and 4) in red show the different nesting green turtle genetic stocks proposed in this study.

Table 1 Mitochondrial DNA variants detected among green turtle populations nesting in 10 different sites in the Southwest Indian Ocean. Haplotype (*h*) and nucleotide diversity (π) for the 10 populations in the North Mozambique Channel (NMC) and South Mozambique Channel (SMC)

	Location	Date of sampling	CM8	C3	May23	D2	Glo33	A1	A2	Total	Haplotype diversity (*h*)	Nucleotide diversity (π)
SMC	Europa	1997/2003	31	2						33	0.1174	0.0076
	Juan de Nova	1999	11	8					1	20	0.5632	0.0360
	Total SMC		42	10					1	53	0.3425	0.0221
NMC	Nosy Iranja	2004		13						13	0	0
	Mayotte	2004	5	30	2			1	3	41	0.4524	0.0231
	Mohéli	2004	1	27	2	1		1	2	34	0.3708	0.0133
	Glorieuses	2004		31			1		7	39	0.3441	0.0168
	Cosmoledo	1996		24				3	4	31	0.3871	0.0210
	Aldabra	1996		18				1	7	26	0.4646	0.0249
	Farquhar	1996		3				1	3	7	0.7143	0.0342
	Total NMC		6	146	4	1	1	7	26	191	0.3964	0.01962
	Tromelin	1997		38					6	44	0.2410	0.0132
	Total		48	194	4	1	1	7	33	288	0.5063	0.0289

Ocean (Fig. 1A and Table 1), that geographically fall into three groups. Those from the South Mozambique Channel (called here SMC) include Europa and Juan de Nova (French Eparses islands); while those from the North Mozambique Channel (called here NMC) include the Mohéli (Comoros), Mayotte (French territory), Nosy Iranja (Madagascar), Glorieuses (French Eparses Island), and three sites in the Republic of Seychelles. The last group,

out of the Mozambique Channel, is composed only by Tromelin (French Eparses Island). In the French Eparses islands, Europa was sampled in 1997 ($n = 24$) and again in 2003 ($n = 9$), for a total of 33 samples; Tromelin ($n = 44$), Juan de Nova ($n = 20$) and Glorieuses ($n = 39$) were sampled, respectively, in 1997, 1999 and 2004. Mayotte ($n = 41$), Mohéli ($n = 34$), Nosy Iranja ($n = 13$) were sampled in 2004. In the Republic of Seychelles, Aldabra ($n = 31$), Cosmoledo ($n = 26$), and Farquhar ($n = 7$) were sampled in 1996.

Typically, the source of mtDNA for the majority of turtles was either skin or blood. Blood samples were taken from the cervical sinus (*after* Owens & Ruiz 1980) and stored in either lysis buffer or frozen in ACD-B (Becton Dickinson solution). Skin samples were taken from either the neck or flipper region and stored in 20% DMSO (Dimethyl Sulfoxide) saturated salt solution (Dutton 1996). All adult turtles encountered in this study were tagged. In some cases, however, mtDNA was obtained from tissues of dead embryos or hatchlings found in the bottom of hatched-out nests (Mortimer & Day 1999) with only one sample per clutch and per female to avoid resampling the same matriline.

Mitochondrial DNA control region extraction, amplification and sequencing

DNA was extracted from small amounts of blood (20 µL) or tissue (0.1 g) by overnight digestion at 56 °C in a 1x TE buffer, proteinase K (0.5 mg/mL) and SDS (0.01%) solution. Digested proteins and cellular material were salted out by centrifugation (17 000 *g* for 20 min at 4 °C) in the presence of Ammonium acetate. The DNA was subsequently pelleted by adding 1 volume of cold EtOH to the supernatant and further centrifugation (13 000 r.p.m. for 20 min at 4 °C). Residual salts were removed by rinsing the DNA pellet twice with 100% and 70% EtOH wash, respectively. The DNA was resuspended in 1x TE buffer. An alternative rapid protocol was also used and involves a proteinase K (0.2 mg/mL) digestion in 0.5 mL of 1x TE buffer and 5% Chelex (Biorad) solution for 4–12 h at 55–60 °C with frequent vortexing. The suspension was heated at 95 °C for 5 min and then centrifuged for 5 min at 13 000 r.p.m. The supernatant was collected and used as template for subsequent polymerase chain reaction (PCR) amplifications.

A portion (~396 bp) of the mtDNA control region was amplified by PCR using the TCR-5 (5′-TTGTACATTACTT-ATTTACCAC-3′) and TRC-6 (5′-GTACGTACAAGTAA-AATACCGTATGCC-3′) primers (Norman *et al*. 1994). Amplifications were performed in a total volume of 25 µL containing 5–50 ng of whole DNA, 10 mM of each dNTP, 10 µM of each primer, 0.5 U of high fidelity Advantage 2 polymerase mix (BD Biosciences) and the corresponding reaction buffer (1x). Cycling parameters were 93 °C for 1 min, followed by 35 cycles at 93 °C for 40 s, 55 °C for 50 s, and 72 °C for 40 s, and a final extension at 72 °C for 2 min (FitzSimmons *et al*. 1997a). Amplification was verified by electrophoresis of 4 µL of each reaction in a 1% agarose gel, together with a 100-bp DNA ladder (New England Biolabs).

Products were purified with the SEQueasy Kleen Kit (Biorad) and run through a 3730XL sequencing analyser (Applied Biosystems). The sequencing reactions (forward and reverse) were performed with dye terminators (BigDye 3.1, Applied Biosystems) on a Primus 96 thermocycler (MWG Biotech).

Data analysis

Sequence alignments were performed with the software CLUSTAL W (Thompson *et al*. 1994). Neighbour-joining analysis (Saitou & Nei 1987) was implemented with the NEIGHBOUR procedure of the program PHYLIP 3.5 (Felsenstein 1993). Bootstrap analysis was computed using of the SEQBOOT (500 replicates) and CONSENSE procedures from the PHYLIP package. The neighbour-joining tree was drawn with the software TREEVIEW 1.5 (Page 1996).

Differentiation between populations was assessed with Wright's fixation index F_{ST} (10 000 replicates; Wright 1951), estimated by θ (Weir & Cockerham 1984) with the GENETIX 4.02 software package (Belkhir *et al*. 2001). This software was also used to estimate the number of migrants per generation (Nm). AMOVA (analysis of molecular variance approach, Excoffier *et al*. 1992) was performed using ARLEQUIN version 2.0 (Markov chain length: 10 000; Schneider *et al*. 2000) to examine genetic structuring among rookeries and among different groups of regional rookeries.

Correlation between genetic (measured as $F_{ST}/(1 - F_{ST})$ following Rousset 1997) and geographical distance matrices was tested with a Mantel nonparametric permutation test (Mantel 1967) as implemented in GENETIX 4.02. The geographical distances between the different nesting sites corresponded to the shortest sea distance between rookeries.

Results

Mitochondrial DNA polymorphism

A total of 40 polymorphic sites were found (Table 2) corresponding to 39 substitutions, one insertion and one deletion. Seven mtDNA haplotypes were observed among the 288 green turtles sampled from 10 rookeries in the southwestern Indian Ocean (Table 1 and Fig. 1A). Six of the seven haplotypes described here have been found elsewhere: CM8 (GenBank Accession no. Z50130) occurs in South Atlantic and West African Rookeries (Encalada *et al*.

Table 2 Polymorphic sites corresponding to the seven green turtle haplotypes detected in the Southwest Indian Ocean from a 396-bp fragment of mtDNA control region sequence

Base positions	32	45	71	82	87	88	89	92	93	95	108	109	110	111	112	135	136	146	147	149
Haplotypes																				
Glo33	T	C	A	G	T	A	C	T	C	G	A	A	T	A	C	G	G	C	T	T
May23	T	C	A	A	T	A	C	T	T	G	A	A	G	A	C	G	G	C	T	T
D2	T	C	A	G	T	A	C	T	T	G	A	A	G	A	C	G	G	C	T	T
CM8	T	C	G	A	T	G	C	C	T	G	A	A	G	C	T	A	A	C	C	C
A2	C	C	A	A	C	G	T	T	T	A	G	G	A	A	C	G	A	C	C	C
A1	C	—	A	A	C	G	T	T	T	A	A	G	A	A	C	A	A	T	C	C
C3	T	C	A	G	T	A	C	T	T	G	A	A	G	A	C	G	G	C	T	T

Base positions	151	153	155	163	222	226	236	248	290	307	328	329	336	343	344	345	347	353	359	360
Haplotypes																				
Glo33	A	C	A	C	C	A	A	G	A	T	A	T	A	T	G	G	T	A	C	—
May23	A	C	A	C	C	A	A	G	A	T	A	T	A	T	G	G	T	A	C	—
D2	A	C	A	C	C	A	A	G	A	T	A	C	A	T	G	G	T	A	C	—
CM8	G	T	G	T	T	G	C	G	G	C	G	T	A	T	A	A	T	G	T	T
A2	A	T	G	T	T	A	A	A	A	T	A	T	G	C	A	A	T	A	C	—
A1	A	T	G	T	T	A	A	A	A	T	A	T	G	T	A	A	C	A	C	—
C3	A	C	A	C	C	A	A	G	A	T	A	T	A	T	G	G	T	A	C	—

1996) and is the first time this variant has been found in the Indian Ocean. Haplotypes C3, D2, A1 and A2 are known to occur in several other rookeries throughout the Indo-Pacific (Dethmers *et al*. submitted; GenBank Accession nos AY955204, AY955205, AY955215 and AY955219, respectively). May23 haplotype was found in the Comoros (Formia 2002) and registered in GenBank as Accession no.. AF529030. A new haplotype is described here for the first time: Glo33 (GenBank Accession no. DQ256086).

The observed seven haplotypes differed by between one and 25 substitutions, corresponding to 0.3–6.5% (mean = 4.2%) estimated sequence divergence. The neighbour-joining tree of the seven haplotypes (Fig. 2) identified three distinct clades of haplotypes: clade 1 (CM8 alone), clade 2 (including A1 and A2) and clade 3 (including C3 and the rare haplotypes May23, D2 and Glo33). The new haplotype Glo33 forms a clade with common C3 haplotype and differs by only two substitutions.

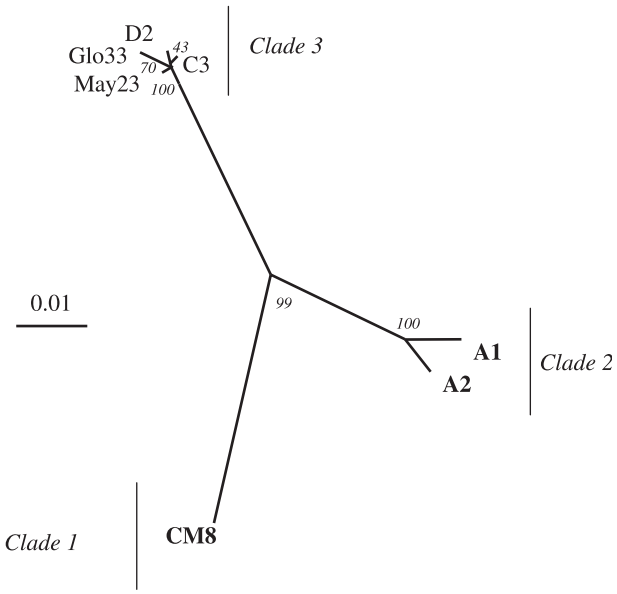

Fig. 2 Neighbour-joining tree based on the mtDNA control region sequences. Bootstrap values (500 replicates) are indicated on the branches. Three clades of haplotypes were identified, called, respectively, 1, 2 and 3. Haplotype Cm8 is nested in the Atlantic Ocean clade B of Encalada *et al*. (1996). Haplotypes A1 & A2 and haplotypes C3 & D2 are nested in the Indo-Pacific Ocean clades V and I, respectively, of Dethmers *et al*. (submitted).

Within-population diversity

Within-population diversity range from one haplotype at Nosy Iranja ($n = 13$) to six (haplotype diversity: $h = 0.3708$; Table 1) at Mohéli ($n = 34$; Table 1 and Fig. 1A). The northern (NMC-Tromelin) regional set of rookeries has higher levels of haplotypic heterogeneity (mean 3.3 haplotypes, $h = 0.3723$) compared to those from the south (SMC, mean 2.5 haplotypes, $h = 0.3425$). All seven haplotypes were found in the NMC rookeries, with C3 at high frequencies, A2 at intermediate frequencies and several rarer haplotypes (CM8, May23, D2, A1 and Glo33). In contrast for the SMC, only three haplotypes were found in Juan de Nova ($h = 0.5632$; CM8 at high frequency, C3 at intermediate frequency and a single occurrence of haplotype

Table 3 Genetic differentiation (F_{ST}) between the 10 locations sampled in the Southwest Indian Ocean (above diagonal) and estimation of the number of migrant per generation (*Nm*; below diagonal). The significance of permutation test (10 000 permutations) are shown for $P < 0.05$ (*) and $P < 0.001$ (**)

F_{ST} *Nm*	Europa	Juan de Nova	Nosy Iranja	Mayotte	Mohéli	Glorieuses	Cosmoledo	Aldabra	Farquhar	Tromelin
Europa		0.3030*	0.9113**	0.6465**	0.7343**	0.7497**	0.7125**	0.7388**	0.7368**	0.8031**
Juan de Nova	1.22		0.5831**	0.3151**	0.4160**	0.4502**	0.5280**	0.3757**	0.4189**	0.5280**
Nosy Iranja	0.03	0.19		0.0793	0.0406	0.0842	0.1742	0.078	0.5011*	0.0466
Mayotte	0.13	0.49	4.46		−0.0106	−0.017	0.0304	0.004	0.1473*	0.0326
Mohéli	0.09	0.32	14.97	∞		−0.0023	0.0374	−0.0111	0.2027*	0.0023
Glorieuses	0.08	0.27	5.07	14.97	∞		0.0035	−0.0112	0.1604	−0.0118
Cosmoledo	0.1	0.39	1.52	7.03	6.43	70.41		−0.0001	0.0124	0.0425
Aldabra	0.09	0.32	4.6	89.66	∞	∞	∞		0.1317	0.0014
Farquhar	0.09	0.54	0.34	1.39	0.98	1.09	19.98	1.65		0.2911*
Tromelin	0.06	0.2	10.17	7.12	106.43	∞	5.63	173.86	0.61	

A2; Table 1) and only two haplotypes were found in Europa ($h = 0.1174$; CM8 in high frequency and C3 in low frequency). Nucleotide diversities on the other hand were similar in both the NMC and Tromelin ($\pi = 0.0184$) and SMC ($\pi = 0.0221$) because most rookeries are comprised of a mixture of divergent haplotypes.

Differentiation among nesting sites population structure

Tests for population differentiation were estimated using Wright's fixation index (F_{ST}) based on haplotype frequency. Results are presented in Table 3. Comparisons between SMC rookeries (Europa and Juan de Nova) and all other rookeries were highly significant [$F_{ST} = (0.307–0.912)$; $P < 0.001$]. There is also a significant differentiation inside SMC between Europa and Juan de Nova populations ($F_{ST} = 0.303$; $P < 0.05$). Farquhar has a small sample size but it is also slightly but significantly differentiated from most other NMC rookeries [$F_{ST} = (0.147–0.501)$; $P < 0.05$] with the exception of Glorieuses, Cosmoledo and Aldabra [$F_{ST} = (0.160–0.012)$; $P = (0.066; 0.340)$]. But all comparisons among the NMC rookeries excluding Farquhar were not significant [$F_{ST} < 0.17 - P = (0.056; 0.610)$]. Comparisons between pooled NMC rookeries and Tromelin were also statistically insignificant [$F_{ST} < 0.0466 - P = (0.081; 0.558)$]. We therefore recognize two genetic stocks in SMC (Europa and Juan de Nova) and a single genetic stock in the NMC comprising Aldabra, Cosmoledo, Glorieuses, Nosy Iranja, Mohéli, Mayotte, Farquhar and Tromelin.

The screening of mtDNA variation shows a frequency shift of haplotypes from Europa to Tromelin Atolls. The CM8 haplotype is the most common in the SMC (Europa and Juan de Nova) whereas the C3 haplotype is most frequent in the NMC (Seychelles, Nosy Iranja, Mohéli, Mayotte and Glorieuses) and in Tromelin. The change in frequency of the CM8 haplotype from south to north Mozambique Channel is particularly informative. It is nearly fixed at Europa (94%), dominant at Juan de Nova (55%), present at Mayotte (12%), rare at Mohéli (3%) and is absent from the other NMC rookeries surveyed (Fig. 1A).

Estimates of gene flow (Table 3) show that there is little exchange between SMC and NMC rookeries ($Nm < 1$) compared to exchange among rookeries within each of these regions (typically $Nm > 1$). There was some evidence for restricted gene flow between Farquhar and some of the more distant rookeries within the NMC rookeries [$Nm = (0.34–1.65)$] compared to the closest rookery Cosmoledo ($Nm = 19.98$).

AMOVA was used to compare four hypotheses about hierarchical structuring among Southwest Indian Ocean rookeries (Table 4). The first model (GP1) had two groups, all the NMC rookeries and all the SMC rookeries. The second model (GP2) had three groups, Farquhar, the remainder of the NMC rookeries and SMC rookeries. The third model (GP3) had three groups, Europa, Juan de Nova and all the NMC rookeries. The fourth model (GP4) had four groups — Europa, Juan de Nova, Farquhar and the remainder of the NMC rookeries. According to among-group variance (F_{CT}) component test results, all four models were statistically significant but the GP3 model explained the highest among group variance (F_{CT}) and is consistent with our earlier identification of just three genetic stocks within this region.

We used a Mantel test to determine if the observed patterns of population genetic structure were consistent with a one-dimension isolation-by-distance model (Fig. 3) and found a significant correlation ($P < 0.001$, $R^2 = 0.3565$; slope = 0.002) between genetic and geographical pairwise distance measures. Concerned that the divergent SMC rookeries might be driving this pattern, we ran the same model without Europa and Juan de Nova and found no correlation between the genetic and geographical distance measures ($P = 0.147$; $R^2 = 0.018$; slope = 0.00004).

Table 4 Analysis of molecular variance (AMOVA) results for the Southwest Indian Ocean groups of green turtle nesting sites. AG is the among-groups component variance; AP/WG is the among-populations/within-group component of variance; WP is the within-population component of variance. The significance of permutation test (10 000 permutations) are shown for $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***)

Name	Grouping scheme	Variance component	% of variance	*F* statistics
GP1		AG	55.84	$F_{CT} = 0.55835$*
Group 1	Europa — Juan de Nova	AP/WG	2.9	$F_{SC} = 0.06562$*
Group 2	Other islands	WP	41.27	$F_{ST} = 0.58733$***
GP2				
Group 1	Europa — Juan de Nova	AG	53.96	$F_{CT} = 0.53959$*
Group 2	Farquhar	AP/WG	2.43	$F_{SC} = 0.05272$*
Group 3	Other islands	WP	43.61	$F_{ST} = 0.56388$***
GP3				
Group 1	Europa	AG	57.18	$F_{CT} = 0.57178$*
Group 2	Juan de Nova	AP/WG	1.46	$F_{SC} = 0.03413$*
Group 3	Other islands	WP	41.36	$F_{ST} = 0.58640$***
GP4				
Group 1	Europa	AG	55.65	$F_{CT} = 0.55653$**
Group 2	Juan de Nova	AP/WG	0.76	$F_{SC} = 0.01720$
Group 3	Other islands	WP	43.58	$F_{ST} = 0.56416$***
Group 4	Farquhar			

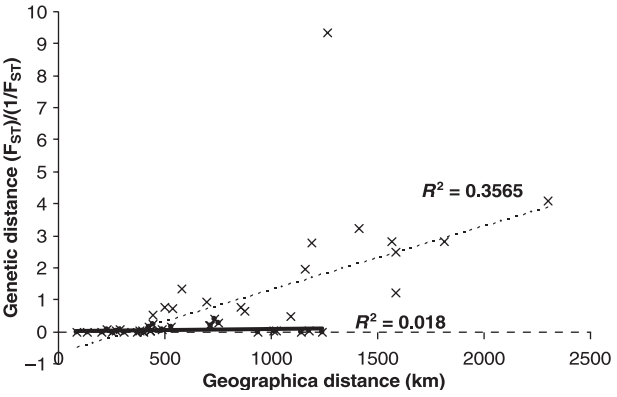

Fig. 3 Regression of genetic distances, $F_{ST}/(1\text{-}F_{ST})$, vs. geographical distances (km) in the 10 green turtle nesting sites sampled for mitochondrial DNA data. Regressions were performed with (×) and without (●) Europa and Juan de Nova.

Discussion

Evidence for gene flow around the Cape of Good Hope

Most of the haplotypes identified in this study conform to expectations and occur elsewhere in Indo-Pacific Oceans rookeries (Dethmers *et al*. submitted) or are novel and occur in low frequency. The remarkable discovery of an Atlantic Ocean haplotype (CM8 Encalada *et al*. 1996) represents the first time that any Atlantic Ocean haplotype has been recorded among any Indo-Pacific nesting populations. The observation of this Atlantic variant mixed with Indo-Pacific haplotypes in a same rookery (Table 1) reinforces the fact that Atlantic and Indo-Pacific lineages are not cryptic species. Until now, several green turtle genetic studies have shown that there is a fundamental phylogenetic split distinguishing all green turtles in Atlantic Ocean and the Mediterranean Sea from those in Indian and Pacific Oceans (Bonhomme *et al*. 1987; Avise *et al*. 1992; Bowen *et al*. 1992). Because of prevailing cold water conditions, the Cape of Good Hope has been commonly assumed to be an absolute barrier to the mixing of Atlantic and Indo-Pacific populations of green turtles but it has not been an impermeable barrier to all tropical species (Briggs 1974).

Had Bowen's *et al*. (1995) total mtDNA study surveyed populations from the Southwest Indian Ocean, they would have found the same remarkable pattern despite the present studies enhanced power using mtDNA sequence data. Using microsatellite data Roberts *et al*. (2004) demonstrated recent or ongoing male-mediated gene flow among populations within Indian and Atlantic Ocean Basins. Although their study did not include samples from the Southwest Indian Ocean it did provide compelling evidence that at least the occasional male was capable of rounding the Cape of Good Hope. Our study of Southwest Indian Ocean rookeries demonstrates for the first time a recent matrilineal link between Atlantic and Indian Ocean green turtle populations. The observation that an Atlantic mtDNA haplotype occurs in adjacent Indian Ocean waters and not vice versa is a significant observation, as it indicates that the direction of matrilineal gene flow is likely to be from the Atlantic to the Indian Ocean. Likewise, the observation that only a single Atlantic haplotype has been

observed and that it occurs in high frequency among SMC rookeries suggests that gene flow is not ongoing. If the Indian and Atlantic Oceans were connected by substantial amounts of contemporary gene flow then we would expect to detect additional Atlantic haplotypes in the SMC. If the colonization event was more ancient then we would expect to have detected novel variants of the CM8 haplotype with our intensive sampling of the SMC region.

A growing number of studies document an Indian and East Atlantic phylogeographical connection in different marine species, like bigeye tuna (Chow *et al*. 2000; Durand *et al*. 2005), hammerhead sharks (Duncan *et al*. 2006), trumpetfishes (Bowen *et al*. 2001) and the urchin diadema (Lessios *et al*. 2001). Almost all cases of marine dispersal in this region are from the Indian to the Atlantic Ocean, usually attributed to passive drift by larvae in the Agulhas Current. However, in a recent study on hammerhead shark (*Sphyrna lewini*), Duncan *et al*. (2006) showed a connection between these two oceans. The authors strongly support that the Indo-West Pacific hammerhead shark haplotypes most closely related to the Atlantic lineage are the product of a recent dispersal from the Atlantic into the Indo-Pacific, and that gene flow in this opposite direction is possible because this species is an active swimmer at every life stage (Duncan *et al*. 2006). Green turtles are also active swimmers at every life stage and may present the second example of active dispersal from the Atlantic into the Indian Ocean.

Regional differentiation

The analysis of the genetic variability of nesting turtles in the Southwest Indian Ocean shows a significant population differentiation between those in the SMC including Europa and Juan de Nova, and the remaining nesting sites that were sampled in the NMC including Mohéli, Mayotte, Glorieuses, Nosy Iranja, Seychelles and Tromelin (Fig. 1A, Table 3). For example, there is a high genetic differentiation (F_{ST} = 0.646, Table 3) between Europa and Mayotte although the two populations are less than 1200 km apart. Inside SMC, there is a significant population differentiation between Europa and Juan de Nova. Our data also show that Farquhar may be differentiated from both rookeries in the NMC (excluding Cosmoledo) and Tromelin (Table 3). This result must be taken with caution as the sample size of Farquhar is small (n = 7) due to the limited number of nesting females present at this remote island when the survey was conducted. However, more intensive sampling may not necessarily lead to the identification of further population genetic structuring here as the well sampled and more distant comparisons of Tromelin and pooled SMC rookeries were also insignificant.

It is rare to see such clear patterns of isolation by distance (IBD) in marine turtles even though it is expected in a species that has natal homing. Our results showed a pattern of IBD (Fig. 3) when run on the entire data set. However there was no relationship between genetic and geographical distance for comparisons among rookeries in the NMC and Tromelin. The decreasing frequency of the CM8 variant from SMC rookeries to NMC rookeries points to IBD operating within the Mozambique Channel but not among rookeries in the rest of the Southwest Indian Ocean. This pattern is consistent with a colonization process whereby rookeries closest to the Atlantic Ocean source populations (e.g. Europa) receive more immigrants than those more distant (e.g. Juan de Nova). In subsequent generations, migration and possible selection could act to further disperse the CM8 lineage throughout the Mozambique Channel beyond the initial founder populations.

Data from turtle tagging studies in the Mozambique Channel (Hughes 1982; Le Gall & Hugues 1987) are consistent with the general observation that most nesting turtles migrate less than 1000 km between breeding and foraging habitat; although distances greater than 2600 km have been recorded for sea turtles (Miller 1997). These observations indicate that the length of the Mozambique Channel is not a biological barrier during the migration of adult turtles. As highlighted by Pelletier *et al*. (2003), we suggest that the unique and unusual oceanography in the Mozambique Channel may contribute to the green turtle population structure observed in the Mozambique Channel, influencing particularly the early stages in the life cycle of green turtles.

Oceanography in the Mozambique Channel

At the seabird nesting islands in the Mozambique Channel, studies have shown that subspecies of *Phaethon lepturus* (Le Corre & Jouventin 1999), *Puffinus lherminieri* (Le Corre 2000b) and *Sula sula* (Le Corre (1999), nesting in Europa (South Mozambique Channel), have phenotypic patterns that differ from the equivalent species nesting in other islands of the Indian Ocean. Le Corre (1999); 2000a, b) suggested that few successful exchanges of individuals occur between the North and South Mozambique Channel and that Europa seabird populations are isolated from the other nesting colonies of the Indian Ocean. This biogeographical pattern may be linked to oceanic conditions in the Mozambique Channel particularly at the south end where there is a peculiar pattern of sea-surface temperatures (Le Corre 2000b).

Several authors have already emphasized the unusual oceanic conditions that occur in the southern Mozambique Channel, where there is an increase of sea-surface temperature (Piton *et al*. 1981), the occurrence of meanders (Lutjeharms *et al*. 1981; Donguy & Piton 1991), and a convergence zone between different currents (Piton & Magnier 1976; Piton & Laroche 1993). Recent studies in the Mozambique Channel showed that the average drift in the

southern part is a dynamic area swept by an intermittent train of large anticyclonic eddies (~200 km in diameter) leading to a southward transport along the African coast (Lutjeharms *et al*. 2000; De Ruijter *et al*. 2002; Schouten *et al*. 2003; Quartly & Srokosz 2004; Fig. 1B. These currents are likely to play a role in hatchling dispersal as they spend the first few years of their life in oceanic waters (Carr 1987). Hatchlings emerging from nests south of the Mozambique Channel should drift southward. On the western side of the Mozambique Channel, oceanic movement consists of strong anticlockwise eddies (De Ruijter *et al*. 2002), whereas on the eastern side the flow is weak and variable. In the northern part of the Mozambique Channel, the flow seems to be quite variable, but on average may consist of an anticlockwise gyre in the Comoro Basin (Lutjeharms 2005). The South Equatorial Current carries water westward in North of the Comoros, but part of this will go south into the Mozambique Channel, part northward as the East African Coastal Current (Fig. 1B; Schouten *et al*. 2003). As Girard *et al*. (in press) have showed that currents around Europa act as a constraint for adult green turtles, one theory would be that juveniles from the NMC do move part northward and part southward, but are mostly retained in this way in the intense western Mozambique Channel eddies. This would mean that they would only occasionally pass close to Juan de Nova and on the whole would not reach Europa Island. A test for this theory would come from the haplotypes found at the Mozambique and southwest Madagascar coasts: if these have Indo-Pacific genetic characteristics, the unusual characteristics at Europa Island would be a localized exception.

Those oceanic elements may contribute to the green turtle genetic structuring in the Mozambique Channel, slowing down the exchanges between these two opposite zones. Further studies are needed to fully elucidate the genetic structure of green turtles nesting along the Mozambique Channel and to distinguish the relative importance of ongoing oceanographic processes from historical patterns of colonization. An expanded study incorporating rookeries from the East African coast, and eastern and southwestern coasts of Madagascar will help us to better understand the mechanisms responsible for structuring among NMC-Tromelin and the SMC green turtle populations. Of particular interest would be the relationships between genetic characteristics of the nesting green turtles, oceanography and seasonality of nesting. For instance, do nesting green turtles in Mozambique coast, at the same latitude of Europa (22°21′S), have the same mtDNA genetic structure as those nesting at Europa?

Green turtle management units

Several rookeries of the Southwest Indian Ocean are important nesting sites for green turtles (Frazier 1984; Mortimer 1984, 1988; Le Gall 1988; Van Buskirk & Crowder 1994; Mortimer & Day 1999). Genetic analysis of sea turtle population structure can provide an essential management tool to identify genetically distinct management units (MUs) within a region (Dizon *et al*. 1992; Moritz 1994). Our genetic data suggest that rookeries of green turtles in Europa, Juan de Nova and the NMC-Tromelin belong to three separate genetic populations and should be considered as independent MUs. Our inability to differentiate Tromelin from other NMC rookeries most likely reflects the limitations of a single locus marker and a recent shared history rather than ongoing gene flow.

The genetic markers we have characterized for each MU are suitable for assessing stock composition in regional harvested and resident populations of green turtle. The assessment of multiple harvests and feeding assemblages throughout this region will help to define the geographical extent of migration and threatening processes that impact on green turtle populations. The delineation of management areas for each MU relies on a combination of tag returns, satellite tracking and genetic analysis of foraging and harvested populations all of which are currently being evaluated for this region.

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CHAPITRE 2 – SECTION 2 : STRUCTURER LES POPULATIONS OFFRE DE NOUVELLES PERSPECTIVES DE GESTION DES TORTUES VERTES DE L'OCEAN INDIEN OCCIDENTAL

POPULATION STRUCTURE ENHANCES PERSPECTIVES ON REGIONAL MANAGEMENT OF THE WESTERN INDIAN OCEAN GREEN TURTLE

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A retenir :

- Exploration complémentaire de la phylogéographie de la tortue verte femelle en reproduction dans le sud-ouest de l'océan Indien
- Analyse des variations de l'ADN mitochondrial de 165 échantillons collectés sur 4 nouveaux sites de reproduction
- Caractérisation de sites au Kenya, au Mozambique et aux Seychelles (Groupes des Amirantes et des Granitiques)
- Suivi par télémétrie satellitaire de 4 tortues en reproduction sur une île des Amirantes
- Hypothèse d'une unité de gestion génétique supplémentaire dans la région, l'unité des Seychelles – SEY
- Les résultats de suivi par satellite confirment cette hypothèse
- Cette unité serait le résultat de jeux de courants liant le Pacifique à l'océan Indien
- Le sud-ouest de l'océan Indien aurait donc *a minima* 3 unités de gestion génétique.

Population structure enhances perspectives on regional management of the western Indian Ocean green turtle

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Running Title*:* spatial structure of Indian Ocean green turtle

Abstract (242 words)

To refine our understanding of the spatial structure of the green turtle *(Chelonia mydas)* populations in the South West Indian Ocean (SWIO), we analysed patterns of mitochondrial DNA (mtDNA) variation among 165 samples collected at five distinct locations (Kenya, Northern Mozambique, and three locations in the Republic of Seychelles: the Granitic, Amirantes, and Farquhar groups) and compared them to genetic data (n=288), previously collected from 10 southern locations in the SWIO. We also analysed post-nesting satellite tracks from four green turtles nesting in the Amirantes group. Pairwise comparisons of haplotype frequencies showed significant genetic differentiation amongst rookeries and suggest that the SWIO hosts two main genetic stocks of nesting green turtles that could themselves divided in two sub-stocks: A. the Southern Mozambique Channel (SMC), that could be composed of two sub-stocks (a1) Europa and (a2) Juan de Nova, and B. the Northern SWIO (N-SWIO) comprising two sub-stocks (b1) the Seychelles archipelago stock - SEY; and (b2) the remaining Northern SWIO rookeries. The newly revealed differentiation of the Seychelles population is supported by restricted migrations of females tracked from the Amirantes group suggesting relatively limited links with other regional stocks. We hypothesize that this differentiation could be due to local and regional current patterns and to the role of the Indo-Pacific Barrier (i.e. the Indo-Australian archipelago) as a genetic break, enhanced during periods of sea level decrease associated with a rare but continuous flow of hatchlings and young juveniles from Western Australia.

1. Introduction

Populations of many large animal species have been severely depleted over the last century (Malakoff, 1997). One of the primary challenges for conservation of widely distributed, long-lived taxa includes assessing status at biologically appropriate scales in order to define conservation priorities. Genetic studies constitute an efficient means to determine effective dispersal and to delineate stock boundaries (Palumbi, 2003). Population genetic analyses have much to offer in unlocking the secrets of the ecology of migratory species, especially in the provision of tools enabling unequivocal species identification, assessment of stocks structure and their connectivity (Avise, 1998). Such techniques have already proven to be effective in fisheries management, despite many marine fishes having long larval periods allowing widespread dispersal in currents and long-lived adults being migratory, further increasing levels of gene flow (Ward, 2000). For example, whereas all tuna species are highly migratory, genetic differentiation has been detected at various scales, within an ocean basin for bluefin tuna (Carlsson et al., 2004), and both within and among oceans for yellowfin tuna (Ely et al., 2005) and bigeye tuna (Alvarado Bremer et al., 1998; Durand et al., 2005). In the case of threatened species, where decisions about management are both difficult and central to species survival, it becomes apparent that information on the genetic differences among populations are important for adequate management (DeSalle and Amato, 2004). The identification of Management Units (MUs) is central to the short-term management and conservation of natural populations (Schwartz et al., 2007).

Marine turtles have been subject to centuries of direct exploitation (Parson, 1962) and therefore are considered species of conservation concern (The IUCN Red List of Threatened Species www.iucnredlist.org; accessed on 19 August 2014). Due to the difficulty of accessing individuals in their marine habitats which can be distributed over thousands of kilometers, knowledge of population dynamics at a regional scale has, until recently, been derived from long-term mark-recapture studies of females flipper tagged while nesting (e.g. Read et al., 2014) or tracked using satellite telemetry (e.g. Hawkes et al., 2012). Such tools provide insights into the population structure and spatial dynamics of individual nesting females, but not necessarily of the population as a whole (Limpus et al., 1992). These studies show that breeding female turtles display high fidelity to their natal nesting beaches (Carr and Ogren, 1960) and earlier Carr (1967) hypothesized that mature nesting females were selecting their natal beach to nest. Several analyses of mitochondrial DNA (mtDNA) structure supported this natal homing hypothesis in the green turtle, as geographically distant rookeries were found to have distinct haplotype frequencies (Norman et al., 1994; Bowen and Avise, 1996), despite extensive overlap of feeding habitats (Bowen et al., 1992).

The mtDNA marker has also proven particularly effective in detecting population structure in marine turtles (FitzSimmons et al., 1999), and several studies have successfully used mtDNA frequencies to resolve population boundaries among breeding green turtles sites separated by more than 150 km in the Atlantic and Mediterranean (e.g. Encalada et al., 1996; Reece et al., 2005), in the Pacific (e.g. Dethmers et al., 2006; Hamabata et al., 2014) and the Indian Ocean (e.g. Bourjea et al., 2007b). The results of these studies made it possible to define discrete Management Units – MU (Moritz, 1994) and to develop Regional Management Units – RMU approaches for marine turtle conservation (Wallace et al., 2010; Wallace et al., 2011).

The South West Indian Ocean (SWIO) is defined here as the waters bounded by the eastern coast of Africa between Kenya and South Africa eastward to 74˚ E, and from 1^{o}S in the North to 30°S in the south. This region hosts some of the most important nesting and feeding grounds for green turtles (Hughes, 1973; Frazier, 1973; 1975; Mortimer, 1984; Le Gall et al., 1986;Le Gall, 1988) and includes major green turtle nesting areas, especially on isolated islands (Frazier, 1984; Mortimer, 1984, 1985, 1988; Le Gall, 1988; Mortimer and Day, 1999; Bourjea et al., 2007a; Lauret-Stepler et al., 2007; Mortimer et al., 2011a, 2011b) that host thousands of females, annually. Nesting of green turtles also occurs on the African mainland and islands of the east African coast, from central Mozambique to

Kenya (Frazier, 1975, 1984; Howell and Mbindo, 1996; Hughes, 1996; Okemwa et al., 2004; Garnier et al., 2012;). However, in Mozambique, Tanzania and Kenya, the status of marine turtles is still somewhat poorly known (Bourjea et al., 2009). Based on available data on green turtles in this region, the SWIO was recognized as a single RMU in the Indian Ocean (Wallace et al., 2011) but there is a paucity of knowledge of how discrete this is from other RMUs in the region.

The mtDNA phylogeography for marine turtles shows a rank-order relationship between thermal preference and evolutionary exchange between the Atlantic and the Indo-Pacific Oceans (Bowen and Karl, 2007), with an ancient separation (d=4.4% in control region sequences; Encalada et al., 1996). However, in the specific case of the SWIO, recent leakage of an mtDNA lineage from the Atlantic into the Indian Ocean has been demonstrated (Bourjea et al., 2007b). These authors also found compelling genetic evidence that green turtles nesting on the rookeries of the Southern Mozambique Channel (SMC) and those nesting in the Northern Mozambique Channel (NMC) belong to separate genetic stocks.

The present study examines the mtDNA polymorphism variation in the SWIO, integrating 15 previously unsampled sites from five distinct locations: Mozambique, Kenya and three locations in the Republic of Seychelles (Granitic, Amirantes and Farquhar groups). We set out to assess any linkages between the known stocks in the Mozambique Channel, the East African coast and the Seychelles islands. We also examine the post nesting migration from individuals tracked by satellite from the Amirantes. The aim was then to use patterns of the results to i) define groups of rookeries that comprise discrete genetic populations, ii) investigate the patterns of subdivision of rookeries in this region and iii) discuss the results from a global conservation perspective.

2. Materials and Methods

2.1 Sampling

Green turtle tissue samples were obtained from 15 sites in the SWIO (Fig. 1, supplement material Appendix A). In Kenya nesting green turtle were sampled using standard protocols (Dutton, 1996) between 2003 and 2006 within a five kilometer sampling site centred on Watamu and Mida Creek, part of the Malindi and Watamu National Marine Parks and Reserves Complex. In Mozambique, samples were collected at Vamizi Island (northern Mozambique, Fig. 1; Garnier et al., 2012) during the breeding seasons 2004 to 2007 using either clean sharp knives (sampling dead turtles), or a 6mm biopsy punch (on live turtles). In Seychelles, samples were collected from three locations including the Granitic, Amirantes and Farquhar groups. All samples were collected either from tagged nesting females, dead nesting females or with due care from dead embryos taking only one sample per clutch and only one per female to avoid duplication of the same matrilineage (supplement material supplement material Appendix A), and using scalpels. Samples were stored in 20% dimethyl sulfoxide buffer saturated salt solution (Dutton, 1996) and frozen until DNA extraction.

Although it is now accepted that female green turtles return to nest on their natal beaches, the geographic specificity of homing is uncertain (Bowen and Karl, 2007; Lee, 2008). Given that the mtDNA control region marker used on green turtles has failed to identify genetic structure among sites separated by less than 150km (reviewed in Bowen and Karl, 2007), small sample sizes from islands closer than 150km (Fig. 1) and displaying similar biogeographic context were directly pooled for analysis to represent five distinct regions: Kenya, Mozambique and three regions in the Seychelles (Granitic, Amirantes, and Farquhar island groups; Table 1; supplement material Appendix A).

2.2 Genetic analysis

The same protocols detailed in Bourjea et al. (2007b) were used to extract DNA from small amounts of tissue (0.1 g) A portion (396 bp) of the mtDNA control region was amplified by PCR (see Bourjea et al. (2007b) for detailed protocol) using TCR-5 (5'-TGTACATTACTTATTTACCAC-3') and TRC-6 (5'-GTACGTACAAGTAAAATACCGTATGCC-3') primers (Norman et al., 1994).
To improve the regional overview of the genetic structure of nesting green turtle in the SWIO, our novel data set was combined with those analysed by Bourjea et al. (2007b; Fig. 1, Table 1). For Farquhar, we combined the samples presented in this study (N=20) with the previous ones (N=7), for a total of 27 samples. We refer in this paper to the Southern Mozambique Channel (SMC) as the area including Europa and Juan de Nova, and the Northern South West Indian Ocean (N-SWIO) as all the other our study sites (Table 1).

Haplotype nomenclature of newly identified haplotypes follows that reported by the Southwest Fisheries Science Center (http://swfsc.noaa.gov/prd-turtles.aspx) for the 384bp fragment with Pacific and Indian Ocean haplotypes being assigned a CmP prefix (Dutton et al., 2008). Sequence alignments were performed with the software DNAMAN V.5.2.2 (©Lynnon BioSoft.) and neighbour-joining trees, based on Kimura 2 parameter distance (Kimura, 1980), were constructed using Mega 4 software (Kumar et al., 2001).

Haplotype (*h*) and nucleotide diversity (π) were calculated for each rookery using Arlequin V.3.5.1. (Excoffier and Lischer, 2010). Pairwise comparison of rookeries was assessed with Wright's fixation index F_{ST} (10 100 replicates; Wright, 1951) estimated by θ (Weir and Cockerham, 1984) and exact tests of population differentiation (Markov chain length: 100000 steps; Raymond and Rousset, 1995) also under Arlequin. The exact test was used here in complement to the conventional F statistic approach as it leads to a more accurate and unbiased test for population differentiation composed of small samples and low-frequency haplotypes (Raymond and Rousset, 1994). Arlequin was also used for analysis of molecular variance (AMOVA; Excoffier et al., 1992) to determine the partitioning of variation within and among rookeries.
In order to visualise the regional structure of nesting green turtles in the SWIO, haplogroup frequencies (i.e. clades) were used to construct isofrequency maps using inverse distance weighted (IDW) interpolation (Watson and Philips, 1985) in ArcGis 10.1. IDW is a deterministic spatial interpolation model that allows interpolation of spatial data and produces visually appealing contour and surface plots from irregularly spaced data and demonstrates expression trends suggested by the data set. This method is simpler than other interpolation methods as it does not require pre-modeling or subjective assumptions in selecting a semi-variogram model (Henley, 1981).

2.3 Satellite tracking

Four adult female green turtles nesting at St. Joseph Island, Amirantes, (5°26'S - 53° 22'E) were fitted with satellite transmitters (two TAM-2639 – Telonics, Inc., Mesa, Arizona; two SPOT-5 – Wildlife Computers, Inc., Bellevue, Washington) in July and September 2012 (supplement material Appendix B). Transmitters were attached to the carapace of the turtles with epoxy resin Pure2k (Powers Fasteners Inc., Wieringerwerf, The Netherlands). All transmitters were programmed to transmit data continuously via the Argos satellite system (CLS, 2014). Location data were filtered following a classic ad hoc heuristic pre-filtering approach consisting of removing 0 and Z class locations, on-ground locations and locations involving a speed exceeding 10 km h^{-1}. Post-nesting migration phases were discriminated by considering temporal patterns of displacement. The start of the migration corresponds to the first date with displacement exceeding 1 $km.day^{-1}$. The end of the migration is considered as the first date after displacement did not exceed $1km.day^{-1}$ for at least 15 days.

Migration paths were smoothed using cubic smooth spline. Foraging area locations were deduced as the centre of all locations post-migration.

3. Results

3.1 Genetic diversity

A total of 165 tissue samples were obtained from 15 new sampling sites and these were pooled to represent five nesting locations in the SWIO: Mozambique, Kenya, and Granitic, Amirantes and Farquhar (Tables 1). Sequence analysis of the 165 samples revealed 41 variable positions defining 12 different haplotypes, 10 of which had been previously described: Cm8 (accession numbers nos. Z50130), C3 (AY955204), C4 (AY955207), C5 (AY955209), IND3 (AF529030), G4 (EU499302), CmP152.1 (KJ502603), A1 (AY955215), A2 (AY955219), CmI7 (EF555561) (Table 1). New haplotypes CMP114 and CMP115 were submitted to GenBank (accession numbers JF314844 and JF314843, respectively).

Haplotype C3 is by far the most common in all 5 nesting areas occurring in 65.7% of the samples, followed by A2 (18.6%) and Cm8 (4.0.%). Cm8 was found in Northern Mozambique (15.8%), Kenya (7.1%) but not in the Seychelles groups. All remaining haplotypes were observed in less than 3 individuals (Table 1). Haplotype diversity (*h*) was highly variable, ranging from 0.143 for Kenya to 0.617 for the Amirantes group with a high average nucleotide diversity (π = 0.023, SD= 0.007) and was comparable to that previously found in this region (Bourjea et al., 2007b; Table 1).
When these results were pooled with data from Bourjea et al. (2007b) there was an addition of two other haplotypes: Glo33 (DQ256086) and D2 (AY955205). The neighbour-joining tree constructed with the 14 haplotypes (Fig. 2) clearly splits the haplotypes into 3 clades (bootstrap value > 0.99). The three Clades are separated by 5.2 – 6.8% mean sequence divergence (Fig. 2) while within-clade divergence was very low (around 0.5%). The neighbour-joining tree also shows that the two new haplotypes (CMP114 and CMP115) found in Amirantes group (Seychelles) are part of Clade 3 (composed of A1 , A2 and CmI7), CMP115 being distinguished from A2 by one substitution and CMP114 by two. Clade 1 is composed of CM8 alone and Clade 2 of C3, C4, C5, D2, G4, IND3, Glo33, CmP152.1 haplotypes.

3.2 Population genetic structure

Population differentiation was estimated using F_{ST} and exact test based on haplotype frequencies between all the sites sampled in the SWIO (see supplement material Appendix C for results site by site). The results show that the newly sampled locations in the Seychelles (Granitic, Amirantes, and Farquhar groups), Kenya, and Mozambique are significantly different from the known SMC Europa (F_{ST} = 0.678 – 0.857; p<0.001) and Juan de Nova stocks (F_{ST} = (0.244 – 0.373); p<0.001). The east African coast locations (Kenya and Mozambique) also show some differences in both F Statistics and exact test from the Seychelles locations but no differentiation from the other N-SWIO locations (F_{ST} < 0.05; p>0.05).

When examining the differentiation within N-SWIO locations, F_{ST} results highlighted a significant differentiation of most of the Seychelles locations from all other ones (F_{ST} = 0.089 – 0.221; p<0.05) even if some discrepancies appear when comparing results from F-Statistics and exact test.
In order to better understand the global regional structure, AMOVA was used to investigate different grouping hypotheses among all sampled locations (Table 2). According to among-group variance, the most significant model was SMC versus all N-SWIO (F_{CT} = 0.592; p<0.001). When removing SMC from the data set, the most statistically significant model was the Amirantes group versus all other N-SWIO

locations (FCT=0.075; P<0.001), followed by the Granitic group, the Amirantes group, Farquhar and Aldabra versus all other N-SWIO locations (F_{CT}=0.065; P<0.001), most of the variance being explained by the within population differences (within population variance > 92%; p<0.01).

In order to further explore genetic structure within our dataset and in agreement with results of AMOVA, we combined geographically proximal rookeries that did not have significantly different haplotype frequencies - i.e. Seychelles (including the Granitic group, the Amirantes group, Aldabra and Farquhar), East Africa (Kenya and Mozambique) and the other N-SWIO locations. Both conventional F_{ST} statistics and the exact test results are in agreement and show strong significant differences between locations (p<0.001; Table 3). When running the same analyses but removing Aldabra from the Seychelles group, the result does not change. However, adding other close locations to the Seychelles Group (e.g. Glorieuses), we lose significance between East Africa or Seychelles and the other N-SWIO locations.

The isofrequency map of haplogroup frequencies (i.e. Clades 1, 2 and 3; Table 1) is shown on Fig. 3. This qualitative approach clearly highlights the already known strongest differentiation between SMC and N-SWIO. It also shows that Clade 2, dominated in frequency by haplotype C3, is commonly found in all SWIO regions while Clade 3 seems restricted within Clade 2 to an area situated in the northeast of the SWIO, mainly in the Seychelles. Such observation is also confirmed by the regional trend in clade frequencies by location (supplement material Appendix D).

3.3 Post-nesting migration

Three of the four turtles tracked from St. Joseph Island exhibited limited movement between breeding and shallow foraging grounds (Fig. 4, supplement material Appendix B). Two turtles (#1 and #4) had their foraging grounds at Desroches atoll, situated only 40 km southeast of St. Joseph; and one turtle (#2) stopped migrating at Platte Island located about 225 km east-southeast of St. Joseph. The last turtle (#3) travelled greater distances to reach her foraging grounds which appear to be situated at Aldabra atoll, some 890 km southwest of St. Joseph. Turtles #1, #2 and #4 each were tracked for more than 65 days at their respective foraging grounds (supplement material Appendix B); so we consider here that these sites were the final foraging grounds of those turtles and not just stopovers in the migration. For turtle #3, the transmission stopped when the turtle reached Aldabra. We are therefore less certain, but hypothesise that Aldabra was her final foraging ground because she reached the shallow waters of the atoll after migrating there in a nearly straight line (Fig. 4).

4. Discussion

The nesting sites sampled in this study encompass most of the major reproductive aggregates of green turtles in SWIO with the exception of those in Somalia, currently inaccessible due to political unrest. Beyond the mid-point of studied locations, the nearest known nesting sites for the species include those that are at least 2600 km away in the Central Indian Ocean (Chagos: Mortimer and Day, 1999); 3100 km away in the Northern Indian Ocean (Yemen: Seminoff and Schroeder, 2007; Oman: Ross and Barwani, 1982); and more than 6000 km away in the East Indian Ocean in Australasia (Australia: Dethmers et al., 2006; Malaysia: Tisen and Bali, 2002; Indonesia: Adnyana, 2003). Therefore, the sampling undertaken is highly representative of the SWIO and provides results that can usefully inform management strategies of this species in the region.

4.1 Genetic diversity

The newly sampled green turtle populations across the northern part of the SWIO showed similar levels of genetic diversity to those previously sampled in this region (Bourjea et al., 2007b), leading to overall similar haplotype diversity. Such levels of haplotype diversity are lower than have been found in the Atlantic (h = 0.83; Encalada et al., 1996) and the Pacific (h = 0.88; Dethmers et al., 2006) and seem to be unaffected by the small sample size. Most of the nucleotide diversity (π) is significantly higher than has been reported from other sites in the Atlantic (e.g. Formia et al., 2006; 2007). Such patterns of variation could be attributed to different colonisation processes over time; but differences in the geographic scale between the present study (< 2500 km) and the studies conducted in Australia and the Atlantic (both spanning > 6500km) make direct comparison unreliable.

Nevertheless, location by location, we found an important variability in haplotype diversity between nesting population sampled in this study, that was comparable to others of similar size range in the Atlantic ($0.0 < h < 0.82$; Encalada et al., 1996; $0.0 < h < 0.73$; Formia et al., 2006), and in the Indo-Pacific ($0.07 < h < 0.82$; Dethmers et al., 2006). Interestingly, some of the highest values of haplotype diversity ($0.52 < h < 0.62$) occurred at nesting locations that host smaller green turtle nesting populations: the Granitic group (<200 estimated clutches; Mortimer, 1984; Bird Island and Ile du Nord Seychelles, unpublished data), Amirantes group (<750 nesters, <3500 estimated clutches; Mortimer et al., 2011b, J.A. Mortimer, D'Arros Research Centre, and Island Conservation Society unpublished data) and Farquhar (less than 1000 nesters; Mortimer, 1984; J.A. Mortimer and Island Conservation Society unpublished data), Juan de Nova (10 – 30 nesters; Lauret-Stepler et al., 2010). In contrast, larger green turtle nesting populations displayed lower haplotype diversity ($0.12 < h < 0.46$): Europa (~2 – 11 000 nesters, ~6000 – 33 000 clutches; Le Gall, 1988); Aldabra (~3 -5000 nesters, ~17 – 18 000 clutches, Mortimer et al., 2011b), Mayotte (~3500 nesters, ~10 000 clutches; Bourjea et al., 2007a), Moheli (~4000 – 6000 nesters, ~12 000 – 18 000 clutches; Bourjea et al., submitted) and Tromelin (~750 – 1000 nesters, ~2100 – 3000 clutches; Le Gall, 1988). Such a finding was previously highlighted by Formia et al. (2006) in Atlantic populations. These authors posited the following possible explanations for higher haplotype diversity in small populations: (1) the combined effects of immigration (e.g. due to imperfect homing behaviour) and recent admixture of distinct populations would have a greater impact on small populations; or (2) the possibility that small populations are remnants of a larger ancestral population in this region. Either hypothesis might explain the patterns documented in the Seychelles and are further developed below.

4.2 Revised phylogeography and population structure

The first genetic study of green turtles in the SWIO found compelling evidence that the green turtles nesting at the rookeries of the Southern Mozambique Channel (SMC) and those of the Northern SWIO (N-SWIO) belong to separate stocks, with the SMC being close to the large Atlantic stock and that could be subdivided into 2 different sub-stocks, Europa and Juan de Nova (Bourjea et al., 2007b). Comparison with SMC and all new N-SWIO locations analysed in this study confirm this finding. Hypotheses explaining these results are discussed in Bourjea et al., (2007b) and will not be further developed here. However, with the new genetic data presented here, the structuring hypothesised by Bourjea et al., (2007b) for the N-SWIO now appears clearer. Most of the Seychelles locations (the Granitic, Amirantes and Farquhar groups) are differentiated from other N-SWIO rookeries and could belong to a separate genetic stock while the East African locations (Mozambique and Kenya) are not. However; the boundary between the Seychelles locations and the rest of the N-SWIO remains unclear.

The difference between the Seychelles archipelago and the rest of the SWIO is also supported by the fact that the new haplotypes found in this study (i.e. CmP114 and CmP115) were found in Seychelles sites and are part of Clade 3 dominant in the Seychelles area. Interestingly, the two other haplotypes G4 and CmP152 also found in Seychelles, while belonging to Clade 2 – the most common clade in N-SWIO sites, were never previously identified in the SWIO before. Haplotype G4 has been previously identified in the Arabian Gulf (Al-Mohanna et al., 2014) and CmP152.1 in western Java (northeast Indian Ocean, M. Jensen & N. FitzSimmons pers. comm.).

Such genetic structure is clearly the consequence of the haplogroup (Clade) frequencies distribution. Clade 1, comprising a single haplotype CM8, is related to an Atlantic lineage (Encalada et al., 1996). It is largely dominant at Europa becoming rare further north. Clade 2 seems to be the dominant clade at all nesting sites sampled north of the Mozambique Channel while Clade 3 is centred in the Seychelles. Clade 2, dominated by the C3 haplotype is widely distributed across the Indian Ocean and Southeast Asia and has limited occurrence in the Pacific Ocean while Clade 3 is mostly found in the Pacific Ocean (Dethmers et al., 2006). Dethmer et al. (2006) suggested that this qualitative dispersal pattern of Clade 2 and 3 was the consequence of intervention by the Torres Strait during geological periods when it was exposed and formed a land barrier between Australia and New Guinea.
In the case of the present study, the question that remains is how to explain the high frequency of Clade 3 only in the Seychelles archipelago while it is in low frequency at all other sites in the SWIO. It is interesting to note that the foraging grounds identified for the four green turtles that nested at St. Joseph (Amirantes group) were also located in and near the Amirantes group (N=3) and Aldabra (N=1). This behaviour differs from that recorded for all other post-nesting green turtles tracked in the SWIO (N=77; Bourjea et al., 2013; Dalleau, 2013) which have been shown to use foraging grounds mainly along the east African and Malagasy coastlines and rarely within the territorial waters of Seychelles archipelago. Such a pattern of short distance migrations is similar to what was found at isolated islands such as the Cocos-Keeling Islands where nesting turtles migrate less than 40 km to reach their foraging ground (Whiting, 2008), and support the hypothesis of limited genetic linkage between the Seychelles area and the rest of the N-SWIO. There may be linkages, however, between Seychelles and the Chagos archipelago located 1600 km east of Seychelles. Four of eight post-nesting green turtles satellite tracked from the Chagos settled on foraging grounds in the Amirantes group (Hays et al., 2014), while one went to the Maldives, one remained in Chagos waters, and two travelled all the way to Somalia (a distance of almost 4000 km). Only limited genetic data are available for nesting green turtles in Chagos, but 44% of nine samples collected and analysed to date (Mortimer & Broderick, 1999; Bourjea et al. unpublished data) can be assigned to Clade 3, thus providing a link to Seychelles. More data on the genetic composition of green turtles nesting in the Chagos are needed to better understand linkages between the SWIO and Chagos. Such a genetic link between Seychelles and Chagos has already been demonstrated for nesting and foraging hawksbill turtles *(Eretmochelys imbricata)* (Mortimer and Broderick, 1999). Vargas et al. (2013) determined that Seychelles and Chagos together form one of nine genetic groupings of nesting hawksbills identified in the wider Indian Ocean (Sheppard et al., 2012).

4.3 Potential role of oceanography

Several authors have already emphasised the important role that oceanic currents may play in structuring the populations of marine organisms in the western Indian Ocean, such as in the phenotypic pattern of sea birds (Le Corre, 1999, 2000), the genetic structure of reef fishes (Muths et al., 2014) or pelagic fishes (Muths et al., 2013). This includes the phylogeography of marine turtles (Bourjea et al., 2007b) as green turtle offspring inhabit drift lines and oceanic gyres while carried by ocean currents during their first several years of life (Carr, 1967). Moreover, recent studies combining genetic data with surface current analyses show that current patterns play an important role in determining the genetic structure of sea turtle foraging aggregations (Carreras et al., 2006;

Bowen et al., 2007; Blumenthal et al., 2009; Godley et al., 2010, Monzón Argüello et al., 2010; Gaspar et al., 2012; Putman et al., 2014).

The possible impact of dominant current patterns in the SWIO on genetic structuring of oceanic populations could also have an important role in the genetic structuring of nesting green turtles observed in the N-SWIO. This region is characterized by the westward flowing South Equatorial Current (SEC), to a large part supplied by the Indonesian Throughflow (ITF). The SEC splits at the east coast of Madagascar near 17°S into the Northeast and Southeast Madagascar Currents respectively NEMC and SEMC; Schott, 2009). The NEMC carries water westward to the north of the Comoros, creating a large anticyclonic seasonal gyre in the Comoros Basin (Lutjeharms, 2005) and part of this flows south into the Mozambique Channel, part northward as the East African Coastal Current (EACC; Schouten et al., 2003). The Seychelles Archipelago comprises hundreds of scattered islands and banks that are distributed across 7° of latitude (from 3°S to 11°S) with the dominant current system being the SEC and the South Equatorial Counter Current (SECC) supplied by the EACC (Piton and Magnier, 1976; Schouten et al., 2003). These currents are present year round, creating a divergence zone with boundaries varying in latitudinal width between 6-7° in austral summer to 9-10° in winter (Piton and Magnier, 1976). Jaquemet et al. (2007) suggested that this divergence zone explained differences in food availability and nesting seasonality of the sooty stern (*Sterna fuscata*) on the Glorieuses Islands south of the South equatorial divergence, and on Cosmoledo located on the edge of the divergence.

The ITF current is known to transport and disperse coral larvae (Knittweis et al., 2009) and therefore probably fish larvae from the Pacific to the Indian Ocean. It follows that the high frequency of Clade 3 in Seychelles might be the consequence of a flow of dominant Clade 3 hatchlings and young juveniles that hatched in the western part of Australia (e.g. Dethmers et al., 2006), Southeast Asia (e.g. in Malaysia; Tisen and Bali, 2002; and in Indonesia; Adnyana, 2003). All such individuals might be derived from colonial nesters that failed to return to their natal beaches to nest, especially during the important environment perturbations induced by the successive exposures of the Sunda Shelf (Voris, 2000). Populations in the Seychelles archipelago that exhibit higher levels of diversity and a high frequency of Clade 3 could be attributed to a combination of imperfect or frustrated homing behaviour and a recent admixture of different stocks.

4.4 Implications for management

It is clear that higher resolution markers would offer greater power to detect stock composition and patterns of movement for the green turtle (Roberts et al., 2004). Microsatellites (or Single Nucleotide Polymorphism) exhibit high levels of length mutation, resulting in extensive allelic variation and levels of heterozygosity (O'Connell & Wright, 1997). These characteristics make them especially suitable for stock identification in species previously exhibiting low levels of detectable variation using mtDNA (see review in Abdul-Muneer, 2014) and will allow unravelling if Juan de Nova could be considered a separate genetic stock as already suggested by Bourjea et al. (2007). Nevertheless, the present study suggests that the SWIO hosts two main genetic stocks of nesting green turtles: the SMC, that could be composed of two sub-stocks (a) Europa and (b) Juan de Nova, and the N-SWIO composed of two sub-stocks (c) the Seychelles archipelago - SEY; and (d) the remaining N-SWIO rookeries. Due to the low number of green turtles nesting in Juan de Nova (< 150 tracks per year, Lauret-Stepler et al., 2010) and the fact that this isolated island is suspected to be a discrete genetic stock, this island has to be considered as a priority site for the conservation of nesting green turtles in this region.

Other green turtle nesting sites of critical concern for conservation are those in the Granitic and Amirantes islands of Seychelles which have suffered and continue to suffer intense depredation due to their proximity to human population centres (>99% of people in the Seychelles live in the Granitic

Islands). We currently consider green turtles from the Granitic and Amirantes groups to be within the same genetic stock, Aldabra and Cosmoledo being a possible mixing area between SEY and the remaining large N-SWIO stock; but what mixing may occur between these sites may not offset the current loss of turtles from the Granitic and Amirantes groups to human exploitation.

The remaining N-SWIO stock spans an unusually large geographic area, 2700 km from Kenya to Tromelin. In contrast, the previously most widely distributed and described genetic stock was only <1200 km in Micronesia (Dethmers et al., 2006). Our study demonstrates a "border effect" within the SWIO of a large stock defined by a mtDNA marker approach (and therefore a limit of this marker), with for example Tromelin being differentiated from North Mozambique (a distance of 1500km straight line) and explained by the low probability of exchange within such huge distances (Bowen and Karl, 2007).

The results of this study can help inform effective management of this species, by contributing to the definition of Management Units (Moritz, 1994; Fraser and Bernatchez, 2001; Wallace et al., 2010; 2011) within this region. What is still lacking, however, are studies of the genetic composition of green turtle aggregations that inhabit the extensive foraging grounds found along the east African and Malagasy coasts, on the Seychelles and Amirantes Banks as well as other shallow sites within the region. Satellite tracking studies (Dalleau, 2013; KESCOM unpublished data; Hays et al., 2014) and flipper tag returns (Mortimer, 2001; J.A. Mortimer and Seychelles Islands Foundation unpublished data; Kelonia/IFREMER unpublished data) clearly demonstrate that these habitats are shared by different breeding populations within the SWIO region and beyond. We consider such a study as a priority for regional management of this important species. As suggested by Godley et al. (2010) an integrated multiple approach is needed that combines genetic analyses of foraging aggregations, with current modelling, as well as satellite tracking and isotope signatures to demonstrate linkages between foraging and breeding habitats (Zbinden et al., 2011). This will lead to an improved understanding of the connectivity and spatial distribution of green turtles and the complexity of their life history.

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742 **7. Figure and Table Legends**

743 **Figure 1:** Geographic locations of the 15 green turtle nesting sites sampled in the South West Indian
744 Ocean. The five new sampled locations are shown in bold italic font. The nine previously sampled
745 sites are shown in regular font (Bourjea et al., 2007b). Numbers of samples per locality are shown in
746 brackets.
747 **Figure 2:** Neighbour-joining tree based on the mtDNA control region sequences of *Chelonia mydas*
748 from the South West Indian Ocean. Newly identified haplotypes are indicated in bold font. Bootstrap
749 values (500 replicates) are indicated on the branches. Three clades of haplotypes were identified,
750 called respectively 1, 2 and 3.
751 **Figure 3:** South West Indian Ocean isofrequency map constructed by inverse distance weighted
752 interpolation method (Watson and Philips, 1985) and using haplogroup frequencies (i.e. Clades 1, 2
753 and 3; Table 2).

754 **Figure 4:** Post-nesting migration paths of four nesting green turtles (#1, #2, #3 and #4) tracked from
755 St Joseph Island, Amirantes, Seychelles. Black circle: departure site; black stars: identified foraging
756 ground: light and dark grey lines: marine turtle tracks. See also Fig. 1 for location details.

Table 1: Mitochondrial DNA variants distribution among green turtle populations nesting at 5 newly sampled locations in the South West Indian Ocean (no shading) and in 10 previously analysed locations (grey shading, Bourjea et al., 2007b). Main genetic stock: N-SWIO = Northern South West Indian Ocean; SMC = South Mozambique Channel. Haplotype diversity (*h*) and (π) nucleotide diversity. Note that Farquhar samples size was increased from n=7 (Bourjea et al., 2007b) to n=27 (present study). Clade 1 is composed of Cm8 haplotype frequency, Clade 2 is composed of C3, C4, C5, D2, Glo33, G4, Cmp152.1 and IND3 haplotypes and Clade 3 is composed of A1, A2, CmI7, CMP114 and CMP115 haplotypes.

Table 2: Analysis of molecular variance (AMOVA) results for the South West Indian Ocean groups of green turtle nesting locations. AG is the among-groups component variance; AP/WG is the among-populations/within-group component of variance; WP is the within-population component of variance. The significance of permutation test (10 000 permutations) are shown for $p < 0.01$ (**) and $p < 0.001$ (***): SMC and N-SWIO: see Table 1.

Table 3: Pairwise comparison of haplotype frequencies ($F_{ST,}$ below diagonal, *: p<0.05, **: p<0.01 and ***: p<0.001; exact P values, above diagonal) between sites sampled in the South West Indian Ocean and pooled into groups (locations): Europa; Juan de Nova; East Africa: Kenya, Mozambique; Seychelles: Granitic group, Amirantes group, Aldabra and Farquhar group; Other N-SWIO: Moheli, Mayotte, Iranja, Glorieuse, Cosmoledo and Tromelin.

Figures and Tables

Figure 1

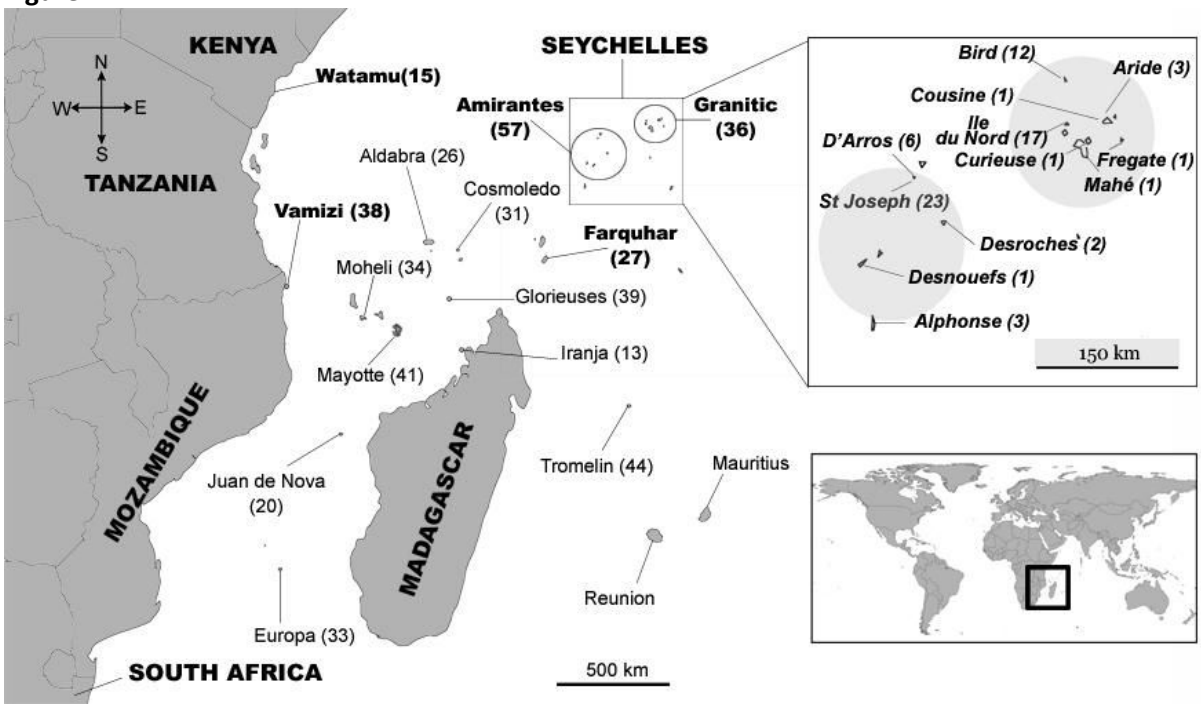
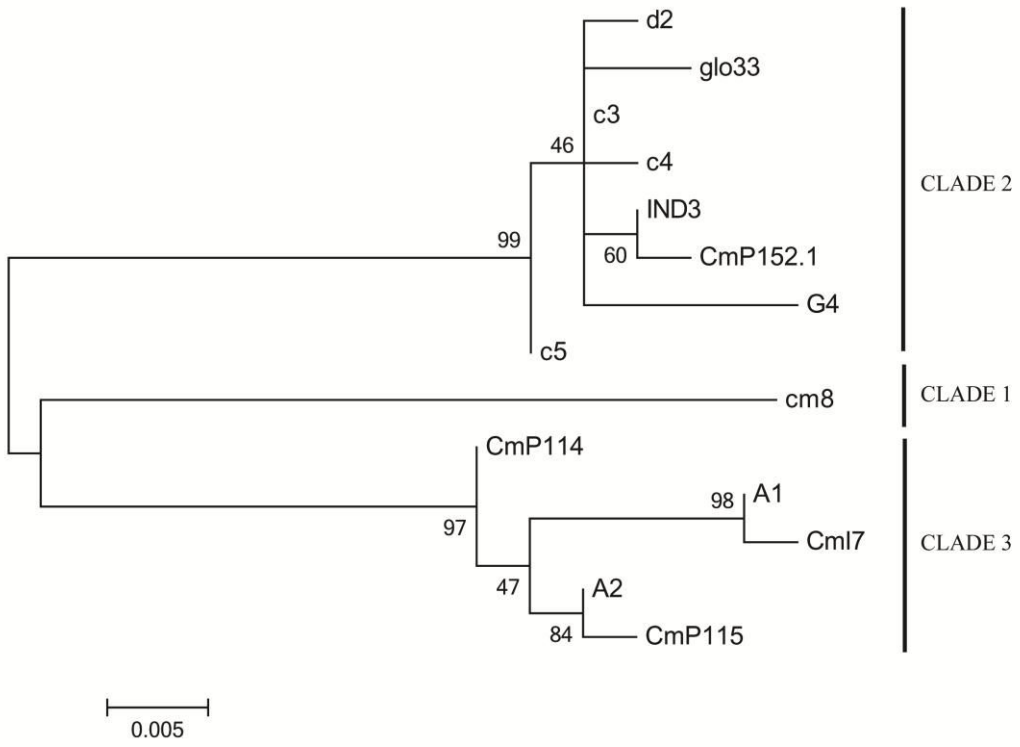
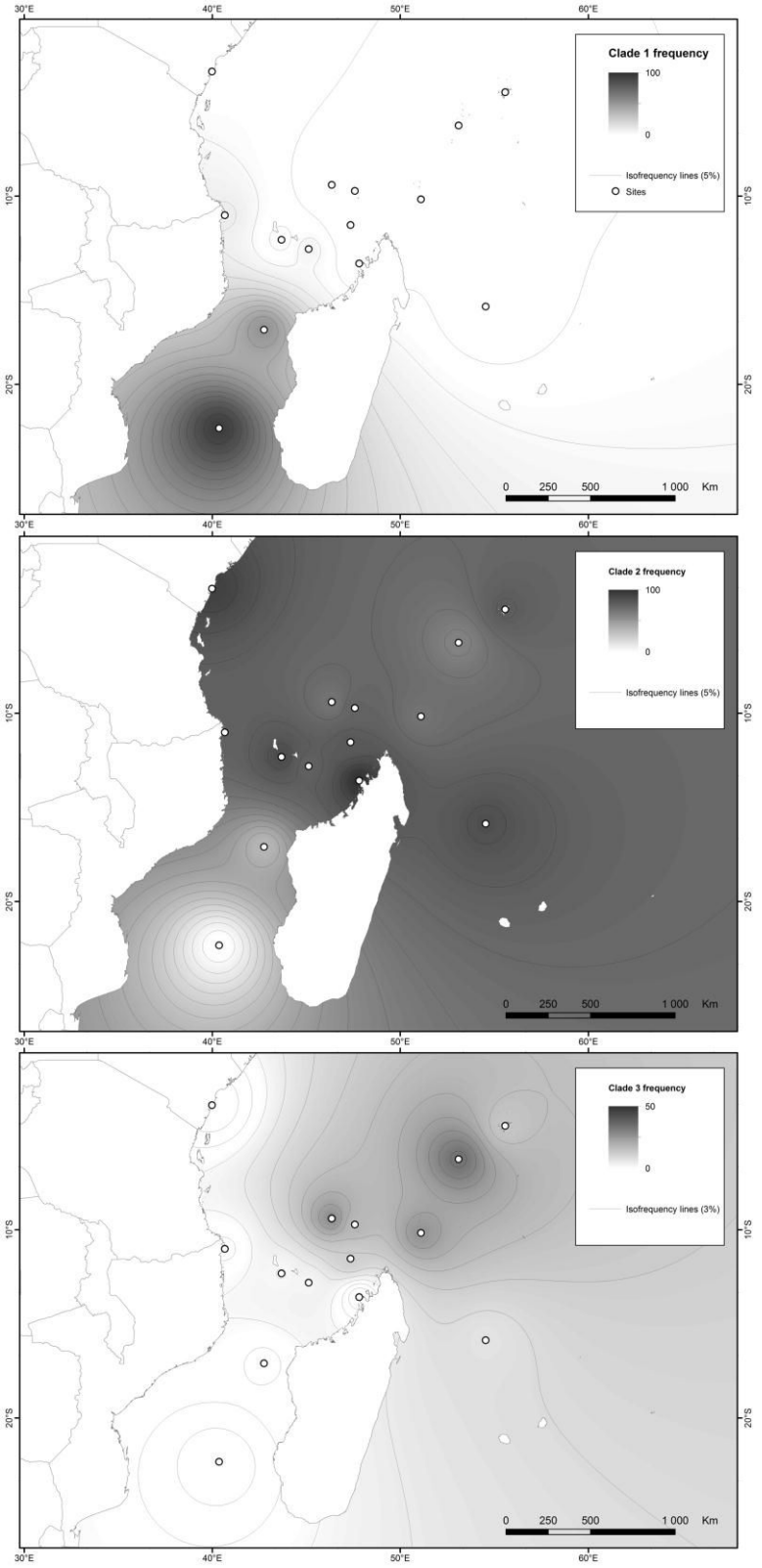


Figure 2



786 **Figure 3:**



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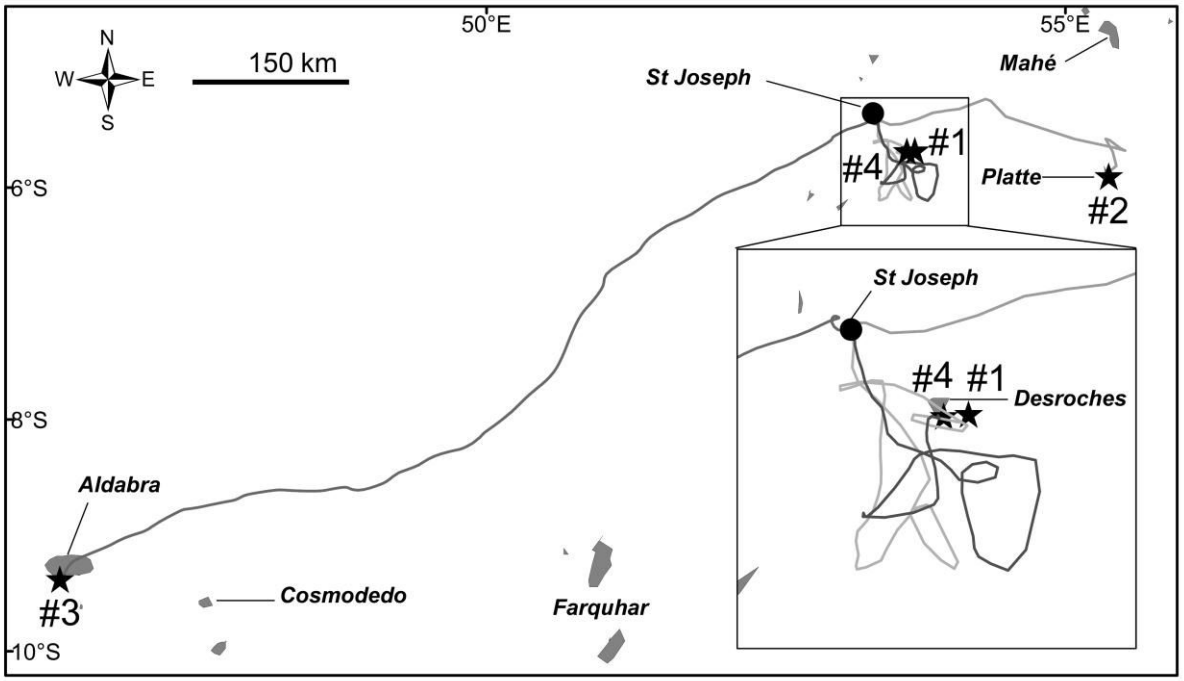
790 **Figure 4:**



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792 **Table 1:**

Main Genetic stock	Location	Cm8	C3	C4	C5	IND3	D2	Glo33	A1	A2	CmP114	CmP115	G4	CmI7	CmP152.1	Total	Haplotype diversity (*h*)	Nucleotide diversity (π)	Clade frequencies (%) Clade 1	Clade2	Clade 3
N - SWIO	**Mozambique**	6	28	1	0	1	0	0	0	2	0	0	0	0	0	38	0.4395	0.0219	16	79	5
	Granitics group	0	23	0	0	5	0	0	0	7	0	0	1	0	0	36	0.5492	0.0182	0	81	19
	Amirantes group	0	31	1	0	1	0	0	1	17	1	1	2	1	1	57	0.6171	0.0268	0	63	37
	Kenya	1	13	0	0	0	0	0	0	0	0	0	0	0	0	14	0.1429	0.0089	7	93	0
	Farquhar	0	18	0	1	0	0	0	2	6	0	0	0	0	0	27	0.5185	0.0245	0	70	30
	Total	**7**	**113**	**2**	**1**	**7**	**0**	**0**	**3**	**32**	**1**	**1**	**3**	**1**	**1**	**172**	**0.5304**	**0.0233**	**4**	**74**	**22**
SMC	**Europa**	31	2	0	0	0	0	0	0	0	0	0	0	0	0	33	0.1174	0.0073	94	6	0
	Juan de Nova	11	8	0	0	0	0	0	0	1	0	0	0	0	0	20	0.5632	0.0347	55	40	5
N - SWIO	**Iranja**	0	13	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	100	0
	Mayotte	5	30	0	0	2	0	0	1	3	0	0	0	0	0	41	0.4524	0.0225	12	78	10
	Mohéli	1	27	0	0	2	1	0	1	2	0	0	0	0	0	34	0.3708	0.0130	3	88	9
	Glorieuse	0	31	0	0	0	0	1	0	7	0	0	0	0	0	39	0.3441	0.0168	0	82	18
	Cosmoledo	0	24	0	0	0	0	0	3	4	0	0	0	0	0	31	0.3871	0.0206	0	77	23
	Aldabra	0	18	0	0	0	0	0	1	7	0	0	0	0	0	26	0.4646	0.0247	0	69	31
	Tromelin	0	38	0	0	0	0	0	0	6	0	0	0	0	0	44	0.241	0.0132	0	86	14
	Over all populations	**55**	**304**	**2**	**1**	**11**	**1**	**1**	**9**	**62**	**1**	**1**	**3**	**1**	**1**	**453**	**0.5154**	**0.0264**	**12**	**72**	**16**

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795 **Table 2:**

Grouping scheme	Source of variation	d.f.	Sum of square	% of variance	F statistics
G1 = SMC locations	AG	1	542.7	59.2	0.592***
	AP/WG	12	141.6	2.6	0.064***
G2 = N-SWIO locations	WP	440	1609.4	38.2	0.619***
G1= Granitic, Amirantes and Farquhar groups, Aldabra	AG	1	53.8	6.54	0.065***
	AP/WG	10	47.2	0.79	0.008
G2 = other N-SWIO locations	WP	389	1437.6	92.67	0.073**
G1= Amirantes group	AG	1	38.6	7.51	0.075***
	AP/WG	10	62.1	2	0.022*
G2 = other N-SWIO locations	WP	389	1437.7	90.49	0.095***

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799 **Table 3:**

FST \ Extact test	**Europa**	**Juan de Nova**	**East Africa**	**Others**	**Seychelles**
Europa		0	0	0	0
Juan de Nova	0.3076***		0	0	0.003
East Africa	0.7294***	0.3079**		0	0
Others	0.6724***	0.3477***	0.1008*		0.025
Seychelles*	0.7515***	0.4436***	0.0230***	0.0584***	

*(Granitic, Amirantes and Farquhar groups, Aldabra)

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CHAPITRE 2 – SYNTHESE : DIVERSITE GENETIQUE, STRUCTURE DES POPULATIONS ET GESTION

Les vertébrés marins présentant une distribution cosmopolite se caractérisent généralement par une importante capacité à se disperser à un ou plusieurs stades de leur vie, impliquant généralement une faible structuration spatiale des populations. Cependant certaines espèces, pourtant considérées comme de grands migrateurs et ayant une capacité de dispersion effective très importante, présentent une reproduction philopatrique, c'est-à-dire une tendance des individus de l'espèce à rester ou à revenir à l'endroit où ils sont nés pour se reproduire. Cette caractéristique favorise la structuration géographique des populations, parfois à de très faibles échelles spatiales. C'est le cas généralement de la mégafaune marine comme pour certains poissons dont le saumon (Dittman et Quinn, 1996), les thons tropicaux (Block et al., 2005) ou les requins (Duncan et al., 2006 ; Castro et al., 2007), les oiseaux marins (Bicknell et al., 2012; Genovart., et al 2013), les cétacés (Hoelzel, 1998; Baker et al., 2013) ou les tortues marines (Bowen et Karl, 2007). Ces connaissances acquises grâce à la génétique des populations deviennent de plus en plus indispensables pour améliorer la gestion des espèces marines migratrices à large répartition (Avise, 1998, Schwartz et al., 2007). La mise en place de mesures de conservation efficaces dépend donc de l'identification d'unités de gestion spatiales et d'information sur l'impact de facteurs extérieurs, naturels ou anthropogéniques, sur les mouvements individuels et/ou les flux de gènes entre ces unités (Palsbøll et al., 2007).

Ce chapitre 2 a pour objectif de comprendre la structure spatiale des tortues vertes dans le sud-ouest de l'océan Indien, d'identifier des unités régionales de gestion pour cette espèce et d'évaluer les relations pouvant exister entre elles ou avec les populations des océans Atlantique et Pacifique. Les travaux qui y sont présentés sont les seuls disponibles ayant été publiés dans l'océan Indien occidental. La structure spatiale des populations a pu être mise en évidence essentiellement en travaillant sur la diversité génétique et le calcul d'un indice de différentiation (F_{ST}) permettant d'estimer la différenciation des populations à partir du polymorphisme génétique (Wright, 1951, Chapitre 2, sections 1, 2). Afin de renforcer les conclusions issues de la génétique, la robustesse de la structure spatiale de cette espèce obtenue par la génétique des populations a pu être évaluée par l'utilisation d'autres approches scientifiques comme par exemple la télémétrie satellitaire (Bourjea et al., 2013; Dalleau, 2013 . Chapitre 2, section 2) ou la modélisation de la dispersion des nouveau-nés (Dalleau et al., 2013).

Les conclusions de ce chapitre permettent aujourd'hui de proposer de manière fiable que les tortues vertes se reproduisant dans l'océan Indien occidental se structurent en deux grandes unités de gestion, l'une dans le sud du canal du Mozambique – SMC, avec une population originaire de l'océan Atlantique et dominée par la Clade 1, et l'autre dans le reste de l'océan Indien occidental – NMC, typique de l'océan Indien et dominée par la Clade 2 ; le centre du canal du Mozambique étant probablement une zone de contact entre ces deux unités (Fig. 2.1). Au sein de l'unité NMC, la zone des Seychelles – SEY, est ce que l'on pourrait considérer comme une sous-population proche génétiquement de l'unité NMC, mais présentant des fréquences haplotypiques différentes, influencées probablement par les populations de tortues vertes de

l'est Pacifique grâce à une structuration des courants océaniques particulière. L'hypothèse d'isolement de cette unité SEY a pu être renforcée par l'observation de suivi par satellite de femelles retournant sur leur site d'alimentation également présent dans cette unité.

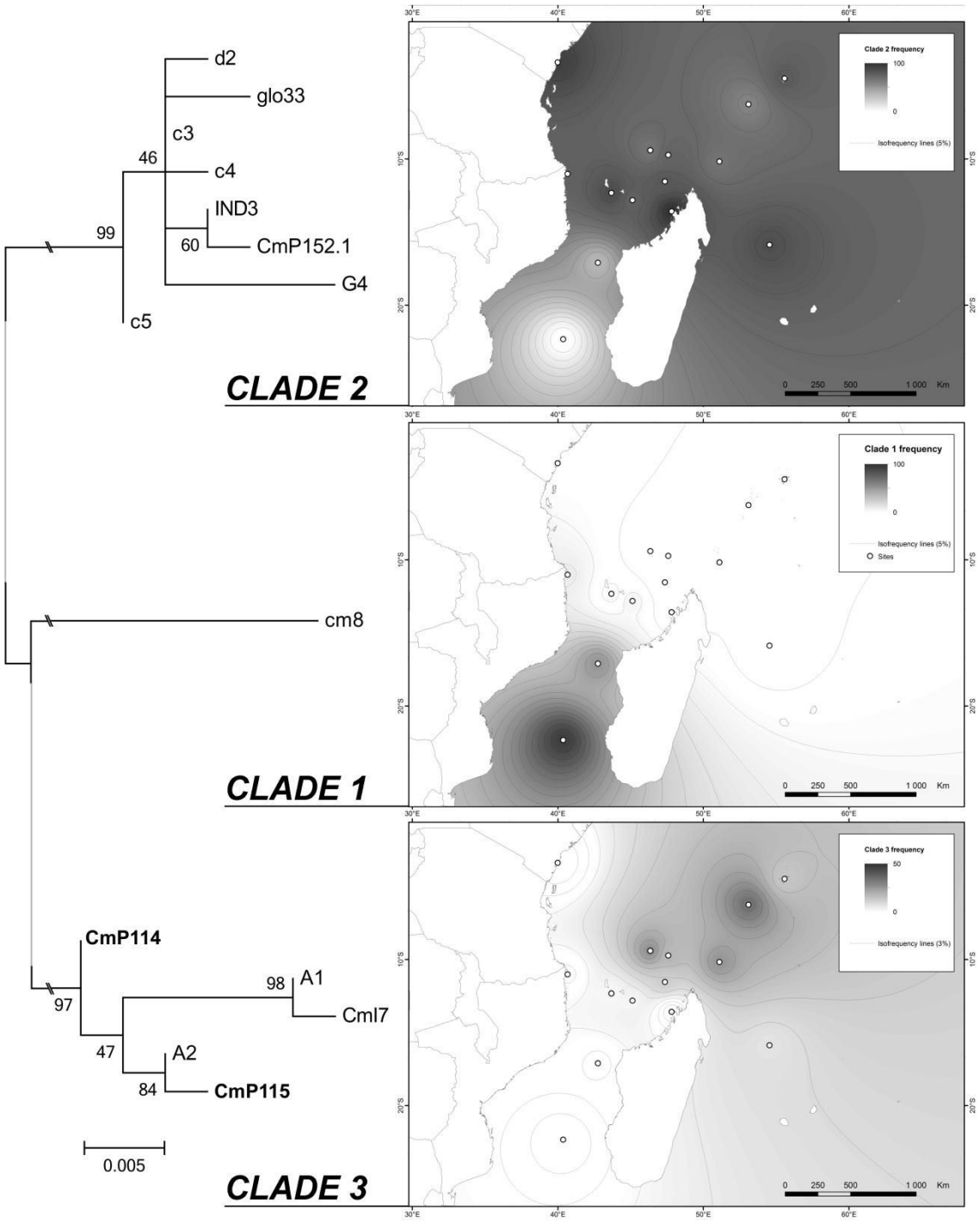

Fig. 2.1 : Structure génétique des tortues vertes dans le sud-ouest de l'océan Indien. Droite : carte des isofréquences des clades de *C. mydas* en reproduction dans le sud-ouest de l'océan Indien. Cette carte a été construire en utilisant la méthode d'interpolation des distances inverses pondérées (Watson et Philips, 1985). Chapitre 2, section 2). Gauche : arbre des plus proches voisins d'haplotypes rencontrés chez *C. mydas* dans le sud-ouest de l'océan Indien (Chapitre 2, section 1, 2). Les traits grisés ont été artificiellement reconstruits pour s'adapter à la figure. Les doubles barres indiquent que la longueur du trait a été tronquée.

Il est important de noter que la diversité génétique d'une population est positivement corrélée à sa valeur sélective (fitness) (Reed et Frankham, 2003), c'est-à-dire sa capacité à se reproduire et à s'adapter de génération en génération aux variations extrinsèques sous les processus de dérive, mutation, migration, sélection. Cette diversité génétique est aussi nécessairement associée à l'effectif de la population. Dans les populations sauvages, tous les individus ne participent pas forcément au processus reproductif, celui qui transmet les allèles des gènes, si bien qu'en général l'effectif de la population «N», qui détermine le rythme de la dérive génétique, n'est pas égal à l'effectif réel de la population. On définit donc l'effectif efficace (ou taille efficace) «N*e*» de la population comme l'effectif d'une population idéale pour laquelle on aurait une fluctuation du polymorphisme équivalente à celle de la population naturelle. C'est donc le nombre d'individus d'une population idéale pour lequel on aurait un degré de dérive génétique équivalent à celui de la population réelle. Or, la taille efficace des populations est un paramètre central en biologie de la conservation car elle permet d'intégrer les effets génétiques aux traits de vie de l'espèce, ce qui permet de réaliser des estimations de «l'état de santé génétique» de cette population (Hare et al., 2011). Elle permet également de se projeter et d'en estimer l'état futur, fournissant un estimateur de la viabilité de la population (Hare et al., 2011).

Une étude récente visant à estimer l'impact de la pêche sur la diversité génétique de 140 espèces de poissons a mis en évidence une chute de la diversité génétique pour de nombreuses populations de poissons exploités, entraînant un impact conséquent sur leur capacité à s'adapter sur le long terme (Pinsky et Palumbi, 2014). Ces mêmes auteurs ont conclu que des espèces exploitées dont la taille efficace était inférieure à 3 000 présentaient un important risque d'érosion de la variabilité génétique. Comme souligné par Allendorf et al. (2014), ce constat est d'autant plus troublant qu'un grand nombre d'autres études ont montré que les tailles effectives de beaucoup d'espèces de poissons étaient inférieures à ce chiffre (Hare et al., 2011).

Dans le cas des tortues marines, la majorité des études génétiques ont porté sur des marqueurs mitochondriaux supposés neutres, permettant de suivre la lignée maternelle, et non nucléaires qui ont l'avantage de couvrir l'information génétique de l'ensemble de la population. En effet, ces études se sont essentiellement focalisées sur des femelles en reproduction pour une meilleure compréhension de la structure des populations nidifiantes ou sur des classes d'âges spécifiques pour établir la composition et l'origine de ces stades sur leur aire d'alimentation (voir discussion Chapitre 2, section 2). Or, ces approches ne permettent pas d'avoir accès à des estimations de taille efficace fiables. Pourtant, ces approches développées dans le cas de l'exploitation des poissons commerciaux par la pêche pourraient être fondamentale pour améliorer la gestion des unités de gestions des tortues marines identifiées dans les trois océans (Wallace et al., 2010a; 2011) et notamment dans l'océan Indien occidental (Chapitre 2).

Prenons l'exemple de l'unité de gestion du SMC composée essentiellement d'une population de 7 – 10 000 femelles de tortues vertes se reproduisant à Europa et dont la tendance moyenne est à la croissance depuis 25 ans (voir discussion chapitre 1, sections 1,2). La perte de diversité génétique ne semble pas être *a priori* être une priorité de gestion. Cependant, sur la base du marqueur mitochondrial utilisé dans ce chapitre 2, on constate que la diversité haplotypique est

extrêmement basse pour ce site (*h*= 0.1174). Cet indice *h* est une mesure de l'unicité d'un haplotype particulier dans une population donnée. Ainsi, plus *h* est élevé, plus il y a de chances d'observer des haplotypes différents chez deux individus sélectionnés au hasard. Dans le cas d'Europa, seuls deux haplotypes ont été découverts, dont un issu de l'Atlantique. Il semble donc indispensable de mieux appréhender quelle est la diversité génétique cryptique réelle hébergée par l'unité SMC en travaillant sur davantage de marqueurs mitochondriaux ou sur des marqueurs nucléaires très polymorphes (microsatellites ou Single NucleotidePolymorphism – SNPs). L'utilisation de ce type de marqueurs permettrait non seulement de mieux évaluer la diversité génétique de cette unité, mais aussi de mieux comprendre et dater les flux de gènes qui se sont opérés entre les océans Atlantique et Indien via le cap de Bonne Espérance (Chapitre 2, section 1). Ces marqueurs nucléaires permettraient en plus de mieux définir les limites des unités de gestion. Ainsi, à l'aide de ces marqueurs nucléaires, une étude récente menée dans le Pacifique sur les tortues vertes en reproduction a permis par exemple de mieux délimiter les unités de gestion pour cette espèce qu'avec des marqueurs mitochondriaux (Roden et al., 2013). Cette approche serait d'autant plus intéressante dans le cas des tortues d'Europa qu'elle permettrait de mieux comprendre les flux de gènes qui s'opèrent avec celles de Juan de Nova.

Le cas de l'unité SEY est également intéressant. Contrairement à l'unité NMC qui est composée de nombreux sites de ponte, chacun accueillant d'importantes populations de femelles en reproduction chaque année, l'unité SEY est composée de peu de sites de ponte, chacun présentant un faible nombre de reproducteurs tous les ans (voir Chapitre 1). L'érosion de la diversité génétique pourrait s'avérer être un problème majeur pour l'avenir dans cette unité, surtout dans un contexte de changement climatique important impliquant de maximiser les capacités d'adaptation dans une population. Pourtant, cette région présente des diversités haplotypiques se situant dans la moyenne pour les tortues vertes ($0.52<h<0.62$; voir Chapitre 2, section 2). Des informations complémentaires apparaissent donc nécessaires à une meilleure compréhension des flux de gènes entre ce site et ses voisins. Réussir à évaluer la diversité génétique de ces populations peu abondantes, et dans tous les cas de figure, la préservation de leur patrimoine génétique compte tenu de leurs caractéristiques génétiques, semble clairement être une priorité pour l'océan Indien occidental.

Nous avons vu que la communauté scientifique est de plus en plus concernée par les conséquences génétiques de l'exploitation des poissons marins (Laikre et Ryman, 1996; Allendorf et al., 2008; Palkovacs, 2011) et les résultats de Pinsky et Palumbi (2014) semblent confirmer une perte importante de la diversité génétique dans de nombreux stocks exploités. Des mesures de gestion peuvent contribuer à limiter cet impact, mais il est impératif que ce problème de l'érosion de la diversité génétique soit pris en compte par les évaluateurs/gestionnaires (Law, 2007). La situation des tortues marines est très probablement similaire. Même si ces espèces ne sont pas des poissons exploités et si elles ne sont pas, ou plus, aujourd'hui la cible de pêcheries dédiées, elles continuent à payer un lourd tribut aux activités humaines, essentiellement liées à la pêche et à la dégradation des habitats, notamment dans le cadre de l'expansion de l'exploration/exploitation pétrolière au Mozambique par exemple. Ce tribut, qui peut être considéré comme un type d'exploitation, a très probablement les mêmes

conséquences que la pêche sur des espèces de poissons. Une meilleure compréhension des niveaux d'exploitation permettrait de mettre en place pour les tortues marines les mêmes types d'approches qui sont actuellement recommandées pour la pêche (Allendorf et al., 2014). La première est «l'évaluation de l'impact sur l'évolution» (Evolutionary Impact Assessment – EvoIA; Jørgensen et al., 2007). Cette approche permet de prédire quel niveau d'exploitation est susceptible d'impacter la diversité génétique de la population, tout en évaluant en quoi ces changements pourraient affecter la productivité de cette population (Eikeset et al., 2013). Dans le cas des tortues marines, cette approche nécessiterait d'abord de disposer d'une bonne évaluation des niveaux d'interaction entre la pêche et ces espèces. Ces estimations sont indispensables pour appréhender l'impact réel de ces prélèvements sur la diversité génétique de ces espèces. Le chapitre 3 de ce manuscrit fournit des éléments clés en ce sens.

La seconde approche prend en compte l'évolution dans le temps de la structure génétique en mettant en place un «échantillonnage génétique» (Genetic monitoring – GeM) qui pourrait permettre de détecter des changements significatifs dans la structure de l'espèce cible (Schwartz et al., 2007). En effet, cette approche permet d'avoir des séries temporelles de résultats génétiques qui pourraient contribuer à mieux comprendre l'évolution des populations (Koskinen et al., 2002; Coulon et al., 2006) et d'anticiper des conséquences irréversibles. Elle permettrait aussi d'observer des changements d'indices de flux génétique, comme les F_{ST}, détectant des changements dans la structure des populations (Ryman et al., 1995), un aspect très important en terme de conservation. Cette dernière approche semble être la plus réaliste à court terme dans le cadre des tortues vertes de l'océan Indien occidental. La mise en place d'un échantillonnage génétique des femelles en ponte dans les sites est une action relativement simple à mettre en place sur ceux déjà suivis au quotidien par les scientifiques (Chapitre 1). Cependant cela demanderait de tester ou développer de nouveaux marqueurs plus performants permettant de prendre en compte le patrimoine génétique de l'ensemble de la population (marqueurs nucléaires), de fournir des tailles de populations efficaces plus réalistes et d'avoir une vision la plus claire possible de la diversité génétique.

Malheureusement dans le cas des espèces en danger, et comme dans la pêche en général (Ovenden et al., 2013), l'approche génétique n'est encore que trop rarement utilisée pour améliorer la conservation de ces espèces «exploitées». Des approches totalement innovantes en cours de développement sur la base d'un modèle biologique exploité (la raie bouclée, *Raja clavata*) et ayant pour objectif de mettre en place un modèle d'identification génétique des «paires de parents-descendants» pour une estimation de la taille absolue de populations en danger (Bravington et al., 2013; Projet ANR GeoPOPTaille 2014) sont à suivre tout particulièrement. Une étude approfondie est cependant nécessaire pour voir dans quelle mesure cette approche est transférable au cas des tortues marines.

CHAPITRE 3 – Estimer les menaces anthropiques qui pèsent sur la mégafaune pour proposer des mesures d'atténuation

Ce chapitre est décomposé en 2 sections et une synthèse.

La section 1 est constituée d'un article présentant un bilan pour l'océan Indien occidental des menaces qui pèsent sur les tortues marines en matière de dégradation des habitats, de braconnage et d'interaction avec la pêche. Cet article propose également des recommandations pour améliorer la gestion de ces espèces fragiles.

Bourjea, J., Nel, R., Jiddawi, N.S., Koonjul, M.S., Bianchi, G., 2008. Sea turtle bycatch in the southwest Indian Ocean: review, recommendations and research priorities. WIO Journal of Marine Science 7(2), 137–150.

La section 2 est constituée d'un article présentant les niveaux d'interaction entre la pêche européenne à la senne océanique et les tortues marines. Cet article évalue l'impact de cette pêcherie sur ces espèces en fonction des modes de pêche, des saisons et des zones géographiques.

Bourjea, J., Clermont, C., Delgado, A., Murua, H., Ruiz, J., Ciccione, C., Chavance, P., 2014. Marine turtle interaction with purse-seine fishery in the Atlantic and Indian oceans: Lessons for management. Biological Conservation 178, 74–87.

La synthèse présente un bilan par pêcherie des interactions avec les tortues marines. Elle compare les niveaux d'interaction avec différents types de pêcheries industrielles (pêche à la senne, au chalut de fond et à la palangre) en activité dans le sud-ouest de l'océan Indien, ainsi qu'avec la pêcherie artisanale de différents pays. Cette synthèse met le doigt sur les problèmes principaux rencontrés pour évaluer ces interactions et propose des pistes d'amélioration pour le futur.

CHAPITRE 3 – SECTION 1 : CAPTURES ACCIDENTELLES DE TORTUES MARINES DANS LE SUD-OUEST DE L'OCEAN INDIEN : SYNTHESE REGIONALE, RECOMMANDATIONS ET PRIORITES DE RECHERCHES

SEA TURTLE BYCATCH IN THE SOUTHWEST INDIAN OCEAN: REVIEW, RECOMMENDATIONS AND RESEARCH PRIORITIES

Auteurs : Bourjea, J., Nel, R., Jiddawi, N.S., Koonjul, M.S., Bianchi, G.

Année : 2008

Journal: WIO Journal of Marine Science

Numéro: 7(2)

Pages: 137–150

A retenir :

- C'est une revue bibliographique de tous les types d'interactions répertoriés entre tortues marines et activités anthropiques dans l'océan Indien occidental
- Cette revue structurée pour 9 pays de la région : Kenya, Madagascar, Maurice, Maldives, Mozambique, Seychelles, Somalie, Afrique du sud, La Réunion, Tanzanie et Yemen
- Trois activités de pêche ont été identifiées comme impactant les tortues marines : le filet maillant, le chalutage et la palangre
- Le manque de données pour beaucoup de pays est le facteur limitant pour pouvoir réaliser des évaluations quantitatives fiables de ces interactions
- Présentation d'une série de recommandations et de priorités de recherche pour l'avenir
- Les plus importantes sont :
    - pourvoir évaluer si un pays est capable d'appliquer les mesures de conservation
    - évaluer si ce pays les applique vraiment
    - mettre en place un suivi de l'impact de ces mesures sur le long terme

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Sea Turtle Bycatch in the West Indian Ocean: Review, Recommendations and Research Priorities

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Keywords: Bycatch, sea turtle, West Indian Ocean, fishery-related mortality

Abstract— Within the framework of the FAO project GCP/INT/919/JPN and a review of published or available data, the relative importance of fishery-related sea turtle mortality in the West Indian Ocean region was assessed for Kenya, Madagascar, Mauritius, Maldives, Mozambique, Seychelles, Somalia, South Africa, Reunion, Tanzania and Yemen. Three fisheries were identified to significantly impact marine turtles: gillnetting, prawn/shrimp trawling and longlining, but it clearly appears that there is a global lack of published and reliable information regarding marine turtle population assessments and interaction with fisheries in the WIO. However, countries such as Seychelles, South Africa and La Réunion (France) already collect various and reliable data that allow an assessment of their marine turtle populations and the level of interactions related to open sea fisheries (mainly longline and purse seine). This allowed the identification of recommendations and research priorities for this region but also demonstrated that such recommendations could only by implemented through the use of appropriate policy measures, adequately designed and developed in cooperation with fishermen, stakeholders, scientists and managers in order to (a) be able to apply the measures, (b) be sure to have the capacity of implementation and (c) be able to provide follow up over time.

INTRODUCTION

Five species of marine turtles are documented from the Western Indian Ocean (Marquez 1990; Ratsimbazafy 2003; Seminoff 2004). Of these, the green turtle (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) are most widely distributed, most numerous, and have been the most severely impacted by directed exploitation (Hughes, 1974a, b; Frazier, 1980, 1982). Loggerheads (*Caretta caretta*) and leatherbacks (*Dermochelys coriacea*) used to be abundant along the South African waters, but less common in the rest of the region, and have had little importance in commerce and directed exploitation (Hughes, 1974a,b). Relatively little has been documented about the olive ridley (*Lepidochelys olivacea*) and is not considered much more that a vagrant species to the region. It was recognised that sea turtles are under pressure from a number of natural and anthropogenic factors, both in the terrestrial phase of their life cycle as well as in the marine environment.

Conservation efforts will only succeed if the major threats can be managed. Little has been done in the South Western Indian Ocean to identify and

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quantify the relative importance of various human pressures. Hughes (1974b) and National Reports to the Indian Ocean South East Asian (IOSEA) Sea Turtle Memorandum of Understanding provide the best overview of impacts in this region. These national reports have highlighted the fact that fisheries interactions with sea turtles constitute a major threat (www.ioseaturtles.org). Furthermore, given the trans-boundary nature of sea turtle populations, a regional approach is essential and overdue.

Within the framework of the FAO project GCP/INT/919/JPN "Interactions between Sea Turtles and Fisheries within an Ecosystem Approach to Fisheries Management", a regional workshop was organised by the Directorate of Fisheries of Zanzibar and FAO to assess the relative importance of fishery-related sea turtle mortality in the West Indian Ocean (WIO) region. The workshop was attended by 31 participants, of which 24 were from 11 countries of the Western Indian Ocean (Kenya, Madagascar, Mauritius, Maldives, Mozambique, Seychelles, Somalia, South Africa, France /Reunion, United Republic of Tanzania and Yemen).

Completed by other regional and available information not presented in the workshop, this review is the result of the cooperation between all these countries that provided grey and reviewed literatures and data available on fishery-related sea turtle mortality in their waters. It is derived from the following main activities: (1) the collation, by country, of quantitative and qualitative information on sea turtle occurrence and general biology, as well as on natural and human-induced mortality; (2) an assessment of the main threats to sea turtles in the region; (3) the evaluation of the potential of a population model to assess the relative importance of the various sources of mortality and particularly of fishery-related mortality on turtle populations; and (4) the determination of priority follow-up activities in the region, related to sea turtle conservation, particularly in relation to fisheries issues.

It remains important to note that information and data presented in this review are composed of 37% of peer reviewed and published literature and 12% of published but no reviewed (proceedings, books, unpublished thesis), 29% of national reports for international organisations (FAO, IUCN, WWF IOSEA and IOTC) and 22% of technical national reports (mainly from reliable and recognized NGO). Therefore, the review presented here, of the available information by country, has to be considered as a rough assessment of the effective population status and interaction between sea turtle and fisheries that occurs in these countries.

PRESENTATION OF AVAILABLE INFORMATION BY COUNTRY

In order to assess the relative importance of sea turtle mortality due to fisheries in the SWIO, representatives from each country received a standard format with 18 categories of data to be compiled and used for assessing major sources of sea turtle mortality. These categories included the legislation frameworks, population census information (Table 1), and information on natural and human-induced mortality and habitat destruction. A complete synopsis of most of the information on sea turtle threats is presented in FAO (2006). As a note, information on the legislation regarding sea turtles for each country is fully presented in the national reports' online facility maintained by the Indian Ocean South-East Asian Marine Turtle Memorandum of Understanding (www.ioseaturtles.org).

Kenya

Sea turtle diversity and status

Kenya's waters host five of the seven species of sea turtles known to occur in the world, the green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricate*), olive ridley (*Lepidochelys olivacea*), loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*). Of these three, the green, hawksbill and olive ridley turtles nest in Kenya (Frazier, 1975; Okemwa *et al*., 2004) while according to Frazier (1975), leatherbacks and loggerheads use Kenya's waters as foraging grounds as well as migratory routes. The marine habitats of the Kenyan coast, which include coral reefs, sea grass meadows and sandy beaches, provide diverse habitats for sea turtles. An aerial survey in 1994 indicated that sea turtles are widely distributed along the coastline within the 20m isobath mainly within sea grass beds and coral reefs (Wamukoya

Table 1. Nesting per species as recorded per country (H>1,000 individuals per annum (ipa); M=100-1,000 ipa and L<100 ipa; ?= No information available). All reports are visible in the website http://www.ioseaturtles.org

Country	*Chelonia mydas*	*Caretta caretta*	*Dermochelys coriacea*	*Eretmochelys imbricata*	*Lepidochelys olivacea*	Legislation	Presenters
Kenya	Nesting (M)	Common in-water sightings	Common in-water sightings	Nesting (M)	Rare nesting (L)	Protected	1
Madagascar	Nesting (?)	Nesting (?)	In-water sightings	Nesting (?)	Nesting (?)	Protected	2
Maldives	Nesting (M)	Very rare sightings	Very rare sightings	Nesting (?)	Rare sightings	10 year ban on adult harvesting. Egg harvesting permitted	3
Mauritius	Nesting outer islands (?)			Nesting outer islands (?)			4
Mozambique	Nesting	Nesting	Nesting				5
Reunion/Eparses Island/Mayotte	Nesting (H)	Very rare sightings	Very rare sightings	Nesting (L)	Very rare sightings	Protected	6
Somalia							7
South Africa	In-water sightings (L)	Nesting (M)	Nesting (L)	In-water sightings (L)	Rare (<1 ipa)	Protected	8
Tanzania	Nesting (M)	Common in-water sightings	Common in-water sightings	Nesting (M)	Rare nesting (L)	Protected	9
Yemen							10

1. Kenya Report: Elizabeth Mueni, Mwaka Barabara, Betty Akunga
2. Madagascar report by Andriamiseza Olga, Rakotomavo Hortense, Rakotonirina Berthin.
3. Hussein Zahir; Sea turtles in the Maldives: Status, threats and management.
4. Meera Koonjul, Veemala Chelumbrun,
5. No report
6. J. Bourjea, F.Beudard, H.Grizel, S. Ciccione – Assessment of importance of sea turtle mortality in the Indian Ocean French Islands
7. No report
8. Nel, Ronel – Turtles is South Africa
9. Asha A.Khatib and Makame S. Nassor (Zanzibar) & Catharine Muir (Tanzania)
10. No report

et al., 1996). Based on a 4-year study from 1997 to 2000, 684 nests were recorded, of which green turtles made up 94% of the nesting activity, with the remainder of the nests comprising hawksbill and olive ridley nests (Okemwa, 2003).

Threats

Important sources of mortality are related to all life stages of sea turtles. Egg predation and nest inundation, together with egg poaching are believed to be the main threats on most nesting beaches. The documented mortality from incidental entanglement in fishing is 18% while pollution contributed 3% (KESKOM unpublished data). Estimated incidental catch rates of turtles in shrimp trawls seems to be as high as 2-3 turtles/day (Mueni and Mwangi, 2001; Mwatha, 2003), and 100 – 500 turtles/ year when Turtle Excluder Devices (TED) were not in use (Wamukoya *et al*., 1997). Information seems also to indicate that the relative mortality due to fisheries either as targeted or incidental is approximately 95% of all documented turtle mortalities in Kenya (Wamukoya *et al*., 1997), with approximately 58% of sea turtles killed as a result of entrapment in fishing nets (Okemwa *et al*., 2004). Other documented sources of mortality are relatively low, with the main constraint being the lack of data on foraging and developmental habitats of the turtles in Kenya and on turtles migrating out of Kenyan waters.

Madagascar

Sea turtle diversity and status

Five species of marine turtle are reported to occur in the coastal waters of Madagascar: the green, hawksbill, olive ridley, loggerhead and leatherback (Marquez, 1990; Ratsimbazafy, 2003; Seminoff, 2004). Only the first four species are known to nest along the coast of Madagascar and the distribution of the nesting sites differs according to each species (Ratsimbazafy, 2003). While marine turtles are commonly exploited by the local population little scientific data is available (Rakotonirina, 2001) and they may be by a variety of human activities including poaching, fishing and habitat disturbance (Rakotonirina and Cook, 1994, Ciccione *et al*., 2002). Several eco-tourism ventures have been established focusing primarily on marine turtles, in areas where nesting occurs, such as in Nosy Iranja Kely, in the north-western of Madagascar that hosts a stable nesting site for green and hawksbill (Bourjea *et al*., 2006).

Threats

Fishers used to take sea turtles for meat (Rakotonirina and Cook, 1994). Direct capture of juvenile and adult turtles of all five species takes place using a variety of gear types. Collection of eggs is also practiced on nesting beaches (Lilette, 2006). Direct capture of juvenile and adult turtles of all five species takes place using a variety of gear types. Mortality due to fishery bycatch takes place both in the traditional (artisanal) and in the industrial fisheries, with the former being the most important (Lilette, 2006). Even if Turtle Excluding Devices (TED) were implemented in some trawls boats to avoid sea turtle bycatches, no records of captures in shrimp trawls were available from Madagascar, but this is probably because there was no effort to document incidental capture of marine turtles (Randriamiarana *et al*., 1998).

Maldives

Sea turtle diversity and status

Five species of sea turtles occur in the Maldives. These being green, hawksbill, olive ridley, loggerhead and leatherback turtles (Frazier *et al*., 2000). However, only two, the green and hawksbill turtles, regularly nest and forage in the Maldives. Little is known regarding population status and abundance.

Threats

High level of exploitation of both eggs and tortoise shell in the past has created conservation concerns that have lead to a decree that bans catching, killing and possession of any species of sea turtles. However, according to Maldives delegates, collection of eggs was not banned and this practice has been a concern for a long time. Fishery-related mortality is largely unknown. Sea turtles reported from Maldives were either entangled in discarded fishing gear or caught incidentally in oceanic driftnets or longlines (Shanker, 2004). The costal reef fishery is not believed to pose a significant threat to sea turtles, while the emerging long-line

fisheries, mainly by foreign licensed vessels, may represent a greater threat as it was already shown elsewhere for these open sea fisheries.

Mauritius

Sea turtle diversity and status

Two species of marine turtles are commonly found in the waters of Mauritius: the hawksbill turtle and green turtle. Nesting of marine turtles is common on all the outer islands, e.g. St. Brandon, Agalega, and Chagos (Mangar and Chapman, 1996). Few nests of these two species were recorded in Mauritius and Rodrigues Islands (Thompson, 1981).

Threats

Natural disturbances such as those due to storms, cyclones and erosion are believed to represent major threats. Illegal egg collection seems to be also an important sources of mortality but no data are available. Even if foreign, open sea fisheries (longline and purse seine) used to operate around and to land enter Mauritius waters, no data are available regarding interaction with sea turtles.

Mozambique

Sea turtle diversity and status

Four species are known to nest along the coast of Mozambique. These are green turtle, hawksbill, loggerhead and leatherback turtles (Gove and Magane, 1996; Louro *et al*., 2006; Costa *et al*., 2007). According to Hughes (1971), the green turtle is widespread but nests north of the tropic of Capricorn, from Quewene Peninsula to the Quirimbas Archipelago. However, the main concentrations of nesting greens occur in the Primeiras and Segundas Islands (Costa *et al*., 2007). Small and immature animals are also concentrated around Bazaruto and Inhassoro and some found in Maputo Bay. Loggerhead and leatherback turtles are more common in the south and nesting beaches are found along the entire coast from Ponta do Ouro to the Bazaruto Archipelago (Hughes, 1971; Costa *et al*., 2007). The most important nesting areas are Ponta do Ouro region, Maputo Special Reserve, Inhaca Island, Quewene Peninsula and Bazaruto Archipelago (Gove and Magane, 1996).

Threats

While costal development presents threats to sea turtles and their habitats, the main threats to these species in this country are related to direct exploitation for eggs and shell (Costa *et al*., 2007). Fishery-related threats, such as entanglement in gillnets, seems to be dominant in Maputo Bay and Bazaruto, while beach seining (using tractors) could be the main threat in Inhassoro. These fishery practices have been estimated to kill on average 30 – 35 green turtles per month in these areas (Hughes, 1971). Sofala Bank is one of the main shallow water shrimp fishing grounds of Mozambique were shrimp trawlers may be a significant source of mortality. Gove *et al*. (2001) estimated over 1,000 deaths per year from this fishery.

La Réunion (France)

Sea turtle diversity and status

The same five species of sea turtles are found in the Indian Ocean French waters but only two species (green and hawksbill) are known to nest in the southwestern French territories (*e.g*. Europa, Juan de Nova, Glorieuses, Tromelin, Mayotte and La Reunion). The green turtle is the dominant species and it nesting population assessments shows overall large nesting populations stable or increasing in the Eparses islands (*e.g*. Europa, Juan de Nova, Glorieuses and Tromelin; Lauret-Stepler *et al*., 2007) and Mayotte (Bourjea *et al*., 2007). In La Réunion Island, nesting started again in 2005 after a 25 years absence and now there are more than 11 green turtle nests recorded in 3 years (Ciccione and Bourjea, 2006).

Threats

The small offshore longline fishery of the French islands (39 offshore longliners in 2006) seems to have a very small impact on sea turtles with very low incidental capture and mortality rates. In 1999, a 3-year study shows that less than 0,004 turtle per 1,000 hooks caught by this fishery (Poisson and Taquet, 2001; Miossec and Bourjea, 2003). Trawling and gillnets are banned in La Reunion. Rare cases of handlines bycatches were recorded the last 6 years (Ciccione, pers. comm.).

Seychelles

Sea turtle diversity and status

Loggerhead, leatherback, olive ridley, hawksbill, and green turtle were also reported to occur in Seychelles (Frazier 1973; 1974), though only the latter two nests in the Seychelles (Mortimer, 1988; 2000a; Hitchins *et al*., 2004). The green turtle nesting is gradually increasing at Aldabra Atoll (Mortimer, 1985) and some other protected areas, but the overall population seems to be decreasing due to a lack of protection on the inner granitic islands (Mortimer, 2000a). Seychelles has the largest population of nesting hawksbills in the western Indian Ocean with about 1 000 – 2 000 nesting females annually (Mortimer, 1984). The hawksbill population, which is most important around the inner islands, is declining due to poaching of nesting females, except at protected sites where there are moderate increases (Mortimer, 2000b).

Threats

According to delegates, poaching of nesting females and loss of habitat and feeding grounds are important threats for hawksbill turtles in the inner islands. Trawls, dredges, driftnets, and shark gillnets have been banned in Seychelles' waters. Fishery-related mortality of sea turtles is probably associated with longlining and purse seining. Even if data are not available for the small longline fishery; Seychelles also host an important European purse seine fleet. Sea turtle bycatch were estimated on the bases of data collected through French and Spanish observer programs representing a total of 1,958 observed fishing sets (Amande *et al*., 2008). Observations of turtles were occasional and almost exclusively made on log-associated tuna school sets (95%). Over the whole period of observations a total of 74 individuals were caught. These observations were mainly reported during the second part of the year when the fishery is actively fishing on Fish Aggregating Devices. Turtle species composition was dominated by three species: *Lepidochelis olivacea,* the olive ridley turtle; *Chelonia mydas,* the green turtle and *Eretmochelys imbricata*, the hawksbill turtle. According to the observations, *L. olivacea* seems the most impacted by the fishery and most of the bycatches occurred in the north–west Indian Ocean (up to the equator). *C. mydas* and *E. imbricata* suffered the lowest bycatch rates and were predominantly caught in the north of Mozambique Channel. Near 90 % of the turtles caught were discarded alive (Amande *et al*., 2008).

Somalia

Sea turtle diversity and status

Green and hawksbill turtles are known to nest extensively along the Somaliland coast (Frazier 1980), but there is no quantitative information on nesting numbers or the exact location of main nesting areas.

Threats

A major source of mortality seems to be related to gillnets used for shark fishing (Nurarale, pers. comm..). Illegal, Unregulated and Unreported (IUU) fishing is probably also a major threat as it seems to be a sub-regional hotspot for these activities, but no quantitative information is available. Traditionally, direct take of eggs and turtles is not practiced in Somalia (Nurarale, pers. comm.).

South Africa

Sea turtle diversity and status

Two species of sea turtles are found nesting along the 200 km north-eastern coast of South Africa, namely loggerheads and leatherbacks (Hughes, 1974a, b; 1993; 1996a,b). Nesting population assessments of these two species indicate that a small leatherback population (about 100 females/ year) also nests in Natal, South Africa (Hughes, 1996a) as well as 100 to 1,000 nesting loggerhead females annually in Tongaland. The eastern seaboard also serves as a feeding and developmental area for hawksbill and green turtles.

Threats

Threats in South Africa are relatively well managed with a virtual absence of direct take. Predation of nest and eggs occur by honey badgers, ghost crabs and water mongoose but is relatively low. Interactions with a number of fisheries do exist

in the South African EEZ. The most important interactions are with longlining operations, small prawn trawl fishery (10% of trawls; Fennesey, pers. comm.) and coastal gillnets (about 50 turtles/year; Young, 2001) with the specific purpose of bather protection against shark attacks. Turtle bycatch in the South African pelagic longline fishery operating in the South African EEZ was recently assessed by Petersen *et al*. (in press) and identified as a key threat to turtle population. A total of 181 turtles were caught on 2,256 observed sets between 1998 and 2005, at a rate of 0.02/1,000 hooks for *Caretta caretta* (60.0% of the total turtle captured), 0.01/1,000 hooks for *Dermochelys coriacea* (33.8%), 0.001/1,000 hooks for *Eretmochelys imbricate* and *Chelonia mydas* (respectively five and three individuals). Even if bycatches occurred in both Atlantic and Indian Oceans, most of them occurred on the Walvis Ridge and on the shelf edge north of the Orange River (25–31 ºS and 0–15 ºE). The catch rates of sea turtles in the swordfish and tuna fisheries differ greatly, with swordfish being far more damaging and catching 89.5% of the marine turtles.

Tanzania mainland

Sea turtle diversity and status

Five species of sea turtles occur off the 900 km long coast of Tanzania: green, hawksbill, loggerhead, leatherback and olive ridley. Of these, only the green and hawksbill nest (Howell and Mbindo, 1996). The key turtle nesting sites, and relative importance, in Tanzania are reported to be Mafia (high), Temeke / Mkuranga (medium), Mtwara (medium) and Bagamoyo / Pangani (low). Approximately 1/3 of the coastline has yet to be monitored. It is estimated that there is an average of 250 – 300 green turtle nests per year and between 5 – 10 hawksbill nests per year (Muir, 2005). However, these figures only represent data for about 1/3rd of the country's coastline. Data on foraging populations and population trends are unknown.

Threats

Main threats to sea turtles include poaching of eggs and habitat disturbance. With regard to coastal fisheries, information gathered from questionnaire interviews and catch monitoring (on Mafia Island) indicate that bottom set 'Jarife' (6-inch mesh) and 'sinia' (12-inch mesh) nets pose a major threat to sea turtles. It has been reported that every turtle captured in both artisanal and commercial shrimp fisheries in the United Republic of Tanzania is killed (Haule *et al*., 1998). The level of mortality from inshore commercial prawn trawlers, pelagic longline and purse seine nets in the Tanzania EEZ is unknown. A total ban on trawling has been implemented subsequent to the FAO meeting, due to reduced prawn stocks, high level of bycatches and commercial non-viability of the fishery.

Tanzania and Zanzibar

Sea turtle diversity and status

All five species of sea turtles occurring in the SWIO are recorded from Zanzibar waters, two of which (green and hawksbill) nest on the island's beaches (Aitchison, 1993; Khatib *et al*., 1996). Important nesting sites for green turtles are Misali (west), Vumawimbi and Kiuyu in Pemba, and Matemwe and Mnemba Islands in Unguja. Nesting population abundance is unknown.

Threats

Zanzibar used to be one of the world's major clearing houses for turtle shell and populations are believed now to be a small fraction of what they once were due to various human impacts, however no past data are available. Tourism development, leading to destruction of nesting beaches, and direct take for meat and medicine, are major concerns for sea turtles in Zanzibar. Information locally-gathered also revealed that in Zanzibar a high incidental gillnet catch rate of green and hawksbill turtles may reach 6 -10 turtles per month (Hamad, pers. comm.). There are about 878 gillnets recorded in 2003 used by fishermen in Unguja and Pemba (Jiddawi and Yahya, 2003). Gillnets were introduced in Zanzibar in the late 1960s (Tarbit, 1984) and their use has increased. Usually fishing is conducted at night during the dark phases of the moon. The drift nets usually targeting large pelagic fish such as king fish, sail fish and tuna can have a length of up to 500-900 m in length with variable mesh size of 7-20cm (Amir *et al*., 2002).

Yemen

Sea turtle diversity and status

Sea turtles are widely distributed along the coasts of Yemen, both in the Red Sea and in the Gulf of Aden. Even if no information is available for the loggerhead turtle, all the other species common in the Western Indian Ocean are found nesting or feeding in Yemen (Walczak, 1979 ; Frazier, 1980; Ross and Barwani, 1982). Large nesting grounds are located at Makulla with more than 10,000 females of green a year but several small nesting grounds are found in the region (Ross and Barwani, 1982). The beach at Ras Sharma is recognized as one of the most important nesting sites along the entire Gulf of Aden, particularly for the green turtle and, to a lesser extent, the hawksbill (Ross and Barwani, 1982).

Threats

The main threats to sea turtles (mainly hawksbill and greens) are suspected to be due to trawling but no data are available.

It clearly appears from this short regional review per country that there is a general lack of reliable information regarding marine turtle population assessments and interaction with fisheries in the WIO (see also Table 1 and 2). However, countries such as Seychelles, South Africa and La Réunion (France) already collect numerous and reliable data that allow an assessment of their marine turtle populations and the level of interactions related to open sea fisheries (mainly longline and purse seine). Even if most of local population assessments still have to be done by each country, most of this available information on the interaction with open sea fisheries from Seychelles, South Africa and La Réunion (France) could be easily extrapolated for modelling to those countries that do not currently collect such kind of data. However, of major concern is the general lack of data and knowledge on costal fisheries interaction, such as traditional gillnets that are known to impact marines turtles and whose impacts should be urgently assessed.

USING MODELS TO ASSESS THE RELATIVE IMPORTANCE OF FISHERY-RELATED SEA TURTLE MORTALITY

In order to carry out population modelling, information on relative magnitude of natality, mortality, emigration and immigration (or dispersal) should be available, and the processes should be understood. Life cycles of sea turtles are particularly complex, given their longevity, delayed maturity, wide geographic distribution, and the use of different habitats, ranging from terrestrial to pelagic, for varying amounts of time throughout their lives. Despite long-term monitoring programmes, such as for green and hawksbill turtles in Seychelles, green turtles from the French Iles Esparses (Scattered Islands), and loggerhead and leatherback turtles in South Africa, the overall conclusion was that data availability in the WIO was very limited – insufficient for thorough population modelling. It was evident that many of the region's countries do not have reliable nesting data and none have comprehensive in-water abundance estimates (Table 1). Furthermore, the data presented showed inconsistencies and lack of standardization in collection protocols.

The second outcome of this analysis was the recognition of the need to standardize current initiatives so that they take place regularly, with set monitoring protocols based on consistent effort and data standards. It was noted that often data are collected without a clear understanding of their usefulness in relation to data analysis, and often lacking a sound statistical basis. For example, many tagging and nest protection programmes are not recording nesting success per sampling effort, which makes the data inadequate for statistical analysis. However, all data and information available on sea turtles, both qualitative and quantitative, were integrated in this analysis they were collected by species, locations, and main sources of mortality.

Fisheries impacts were scored per species for each life history phase, with the lower the score the more important the threat. Table 2 shows the threats due to fisheries for each of the five turtle species. In the WIO, coastal fisheries, mainly gillnets,

Table 2. Incidental take in fisheries in the West Indian Ocean (threats ranked: 1-5) for five species of turtle. Each species was scored per life history phase, and the lower the score the more important the threat. Data collection is detailed in FAO (2006)
1 = High threat level; high importance to take action; 2 = Medium threat level; 3 Low threat level; low importance to take action; 4 = No threat level; N/A = Not applicable, ?(X)= No information available but suggested level of threat

	Leatherbacks			Hawksbill		Green		Loggerhead		Olive Ridley	
	Adult	Juvenile	Hatchling	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Incidental take in fisheries											
Longline (shallow and deep-set)	2	2	4	?(2)	?(2c)	2?	2?	1.5j	1.5j		
Demersal longline	2	2		?(2.5)	?(2.5)			4k	4k		
Purse seine	3.5?	3.5?	4	3.5	3.5	4	4	4?	4?		
Trawl	3.5	3.5	4	3.54	3.54	2.5f	2.5f	2.5	2.5	2	2
Coastal fisheries (gillnet)	2.5a	2.5a	4	2	2	1	1	2	2	2	2
Pound nets/traps/pots	4	4		3.5	3.5	3	3	4	4	3	3
FAD-based fishery	?3b	?3b		2.5?	2.5?	4?g	4?g	2.5?	2.5?	3	3
Hook and line	3.5	3.5		3.5	3.5	3.5	3.5	3	3		
Dynamite fishing	4	4	4	4d	4d	4h	4h	4l	4l	3	3
Spearing	4	4		4e	4e	4	4	4	4		
Drift-netting	4	4		4	4	?	?	4	4		
Poison	4	4		4	4	3	3	3.5	3.5		
Beach seine netting	4	4		4	4	4i	4 i	3.5	3.5		

a Specific to Tanzania, and the special case of bather-protection nets in South Africa.
b Specific to Seychelles.
c South Africa & Reunion (4)
d Tanzania (2)
e Kenya (3) & Zanzibar (2)
f Trawling more important in Kenya, Yemen and Tanzania.
g Region has a large purse seine FAD driven fishery (emerging issue)
h Rating of 2 for Tanzania/Zanzibar
i Rating of 3 for Mozambique
j South Africa good data between 2000-2004; a 43% bycatch on Cc; no other member state had data.
k South Africa not considered a problem; other member states no data.
l Zanzibar (2) & Yemen (3)

seem to have the highest impact on sea turtles, with a particular relevance to green turtle (Table 2). Trawlers appear to mainly threaten turtles that have a more coastal behaviour (namely green and hawksbill) whereas turtle species which display more pelagic behaviour during all their life stages seem to be more impacted by longlines (namely leatherback and loggerhead). Although there are limited data regarding turtle interactions with purse seine fisheries using drifting Fish Attraction Devices (FADs), a recent report shows that the level of bycatch remains low (Amande *et al*., 2008). However, the use of pieces of net, hung below the FADs, has to be banned as they are believed to be a cause of mortality of sea turtles due to entanglement and subsequent drowning. Mesh size of these net fragments used by such FADs appeared to be a key contributing factor (Amande *et al*., 2008). It is recommended that net material should be replaced with materials such as non-plastic ropes or non-plastic hoods or straps that will not entangle sea turtles.

BALANCING TREATS, MITIGATION MEASURES AND THEIR APPLICATION TO MARINE TURTLES

There are currently 141 sites of importance identified across 10 nations in the WIO that provide nesting, developmental and feeding habitats (www.ioseaturtles.org). The conservation efforts that are taking place across these sites are summarised into 10 categories ranging from monitoring programmes, to building restrictions and fishing gear modifications (Figure 1). The most commonly employed conservation measures are Marine Protected Areas (26%) accompanied by *in situ* monitoring (24%), and education and awareness programmes (23%). Hatcheries and egg relocation is reported for 10% of the sites. This is in agreement with the fact that direct take (nesting turtle poaching, egg harvesting), is the currently known to be the largest threat to sea turtles across the region. In fact, fishing gear modifications are reported to be used in only 6% of the cases, which is the lowest of all mitigation measures (Figure 1).

It is important to view the impacts of fisheries in the light of other land-based or coastal threats. It is clear that, despite strong legislation prohibiting the direct take of turtles throughout the entire WIO, it is still regarded as the most important threat. An evaluation of the level of take and impact thereof indicated it to be moderate to high in eight of the 11 countries, affecting all of the species (www.ioseaturtles.org). This impact scored higher than any of the fisheries impact ratings (see Table 3).

Appropriate conservation policies to address threat to turtles in the WIO should be require legislation but can only by implemented if they are adequately designed and developed with all stakeholders (namely fishermen, scientists and managers) in order to gain consensus. The capacity to implement such measures must exist locally (and regionally) and follow-up over the short-term and long-term is paramount to achieving success. Without such an approach, these policies are unlike to have any effects on turtle populations. This should be of major concern, especially in countries where priorities are not biodiversity conservation but more socio-economic development.

RECOMMENDATIONS AND IDENTIFICATION OF RESEARCH PRIORITIES

There are four current focus areas suggested for future research and management activities. Firstly, regarding fishery-related threats, the impacts of three fisheries were identified as significant: gillnetting, prawn/shrimp trawling and longlining, leading to a number of recommendations/priorities. These are: Ihe lack of quantitative data is the greatest weakness and therefore should be addressed at all levels, incorporating artisanal and industrial fisheries, and should involve local communities, fisheries administrations, and regional fisheries management organizations (RFMO); 2) research that will highlight turtle-fisheries interactions that could potentially lead to the reduction in bycatch, such as time-area closures, should be promoted; 3) trained-observer programmes should be initiated to collect data on both local and foreign fishing fleets; and 4) experimentation with mitigation measures, including TEDs and circle hooks should be encouraged.

The second focus area relates specifically to illegal, unreported and unregulated fisheries (IUU) as this was a frequently raised issue. While

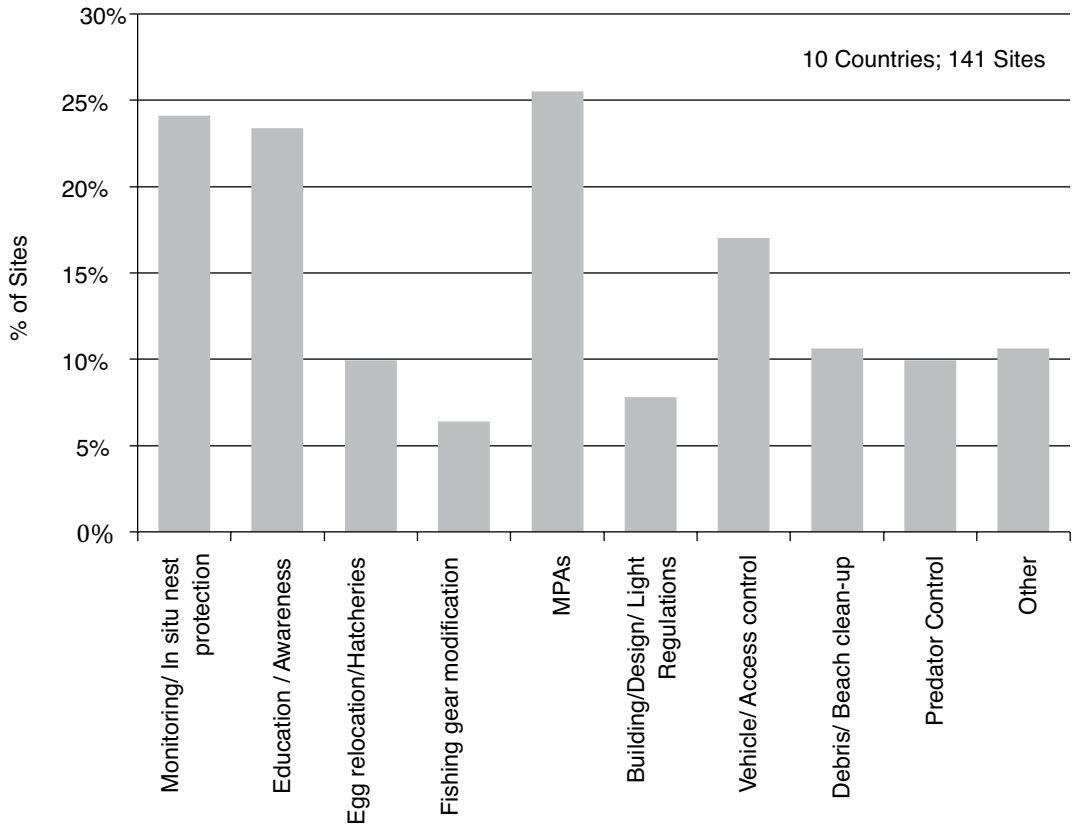

Fig. 1. Mitigation measures used to reduce impacts on sea turtles and their habitats in the Western Indian Ocean. All reports are available on the website http://www.ioseaturtles.org

Table 3. Evaluation of the level of take and impact in the dominant species nesting in the countries of West Indian Ocean (IOSEA database; All reports are available on the website http://www.ioseaturtles.org)

	Dominant Species Nesting	Level	Impact
Comoros		Moderate (2)	Moderate (2)
France (les Iles Eparses, La Réunion, Mayotte)	Cm	Moderate (2)	Moderate (2)
Kenya	Cm	Moderate (2)	Moderate (2)
Madagascar	Cm/Cc/Ei	High (1)	High (1)
Mauritius	Cm	?	?
Mozambique	Cm/Cc/Ei/Dc	High (1)	?
Seychelles	Cm/Ei	High (1)	High (1)
Somalia	Cm	?	?
South Africa	Cc/Dc	Incidental (3.5)	Incidental (3.5)
United Kingdom (Chagos)	Ei	None (4)	None (4)
Tanzania	Cm	Moderate (2)	Moderate (2)

Cm= Chelonia mydas; Cc=Caretta caretta; Ei=Eretmochelys imbricata & Dc=Dermochelys coriacea

it is recognized that the problem of IUU is being addressed in Ir fora, such as under FAO initiatives, it is important to explicitly emphasize that resolving this complex issue is intimately related to mitigating problems of sea turtle bycatch. Based on that, the national administrations were encouraged to review, improve, harmonize and enforce legislation on turtles whereas RFMOs and national administrations were encouraged to recognize the potentially significant impacts of IUU fishing on sea turtle populations in the region (especially for Somalia and Tanzania).

The third focus area relates to the biology and ecology of sea turtles. Studies are encouraged to provide information on long-term abundance and nesting trends, but these should be conducted in a structured, scientifically robust manner. Training programmes and capacity building will be the basis of this focus. More complex questions, such as genetic stock structures and population dynamics of sea turtle stocks in the region (including hatching success, sex ratios, and natural mortality), should be addressed. This will, however, require collaborative research, as suggested by FAO (2006).

The fourth and last focus area relates to the socio-economic complexities of the region. Participants from each country identified turtle catches, direct or bycaught, to be intimately dependent on social, economic, and political forces. It was thus recognised that sustainable fisheries and an ecosystem approach to fisheries management is to be obtained if socio-economic, cultural and resource use studies are included in future research plans. Without resolving root issues of livelihood, resource access and governance, even the best attempts at technological advances, such as gear modifications, will have limited success (FAO, 2006).

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CHAPITRE 3 – SECTION 2 : INTERACTION ENTRE LES TORTUES MARINES ET LA PECHE THONIERE OCEANIQUE DANS LES OCEANS ATLANTIQUE ET INDIEN : LES LEÇONS A TIRER POUR LA GESTION

MARINE TURTLE INTERACTION WITH PURSE-SEINE FISHERY IN THE ATLANTIC AND INDIAN OCEANS: LESSONS FOR MANAGEMENT

Auteurs : Bourjea, J., Clermont, C., Delgado, A., Murua, H., Ruiz, J., Ciccione, C., Chavance, P.

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A retenir :

- Evaluation des interactions entre la pêche thonière à la senne océanique européenne et les tortues marines dans les océans Atlantique et Indien
- Analyse de 17 ans de données d'observateurs embarqués sur les thoniers
- Les résultats indiquent que la pêche à la senne océanique a un impact très faible sur les tortues marines
- Une analyse fine des interactions entre les Dispositif de Concentration de Poissons (DCP) dérivants et les tortues marines a également été menée
- Les résultats indiquent que les DCP jouent un rôle clé dans l'agrégation des tortues marines juvéniles
- Ils indiquent également que les DCP ne sont pas la principale source de mortalité pour ces espèces.

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Marine turtle interaction with purse-seine fishery in the Atlantic and Indian oceans: Lessons for management

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ABSTRACT

Bycatch of endangered marine turtles is a growing issue for the management of all fisheries, including the oceanic purse-seine fishery. The aim of this study was to assess the spatial and temporal variation in bycatch rates of these species in the entire European purse-seine fishery operating in the Atlantic and Indian oceans. The study was based on data collected through observer programs from 1995 to 2011. During that period, a total of 15 913 fishing sets were observed, including 6 515 on Drifting Fish Aggregating Devices (DFADs) and 9 398 on free swimming schools, representing a global coverage of 10.3% and 5.1% of the total fishing activity in the Atlantic and Indian Ocean, respectively. Moreover, from 2003 to 2011, 14 124 specific observations were carried out on DFADs to check turtle entanglement in the net covering DFADs. We found that the purse-seine fishery has a very low impact on marine turtles. We estimated that the annual number of individuals incidentally captured was 218 (SD = 150) and 250 (SD = 157) in the Atlantic and Indian Ocean, respectively, with more than 75% being released alive. The present study also investigated the impact of DFADs; which is considered a key conservation issue for this fishery. Drifting objects may play a key role in aggregating juveniles of marine turtles, implying the need for improving their construction to avoid entanglement (e.g. avoiding nets in the structure); however, based on our study it is not the main source of incidental captures of marine turtles in this fishery.

1. Introduction

Marine ecosystems are extensively affected by human activities and require urgent implementation of management and conservation measures for marine resources (Halpern et al., 2008). The environmental and economic concerns about the impacts of fisheries on these ecosystems and associated marine populations are growing. Fisheries can alter habitats, and disturb the community structure by increasing mortality and modifying the population composition which consequently, may affect the whole ecosystem (Jenning and Kaiser, 1998; Hall et al., 2000; Jackson et al., 2001; Pauly et al., 2005). Bycatch, *i.e.* the incidental catch of undesirable size or age classes of the target species (e.g. juveniles), or the incidental catch of other non-target species (Lewison et al., 2004) has such negative impact. Large marine vertebrates, such as marine turtles, marine mammals and seabirds, with little or no commercial value, accidentally interact with a large range of fishing gears, resulting in injury or possible individual death (Hall et al., 2000). However, assessing the real impact of bycatch on large marine vertebrate populations is challenging. Sea turtle bycatch tends to be a relatively rare event, with most observed fishing sets containing zero bycatch, and most events clustered within the relatively few sets that overlap animal aggregations (Sims et al., 2008).

Six of the seven marine turtle species are listed as Vulnerable, Endangered or Critically Endangered on the IUCN Red List (www.iucnredlist.org; accessed 30 July 2012). Marine turtles are captured in most of fishing gears (Alverson et al., 1994) but little is known about the real level of associated mortality. The long

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oceanic migration of most marine turtles (see review in Luschi, 2013) leads them to interact with open ocean fisheries worldwide; however, the lack of global understanding of the movement between the successive habitats and the level of interactions with fisheries preclude the implementing of appropriate management measures to significantly reduce fisheries related mortality. A need of a "region-gear" combination that warrant urgent conservation measures needs to be adopted.

Tuna (or swordfish) drifting longline fishery, the drifting gillnet fishery and the oceanic purse-seine fisheries are among the most economically valuable open sea fisheries in the Atlantic and Indian oceans. In both oceans, information is available regarding interaction with marine turtles for both longline and gillnet fisheries (see Hall et al., 2000; Lewison et al., 2004; Moore et al., 2009; Wallace et al., 2008, 2010; Lewison et al., 2014), but little is currently published regarding the real impact of the purse-seine fishery on marine turtles. In 2012 the fishery recorded around 307 000 tons of tuna in the Atlantic and 356 000 tons Indian Ocean and is dominated largely by the European Union (EU) fleets composed of Spanish and French vessels. The purse-seine fishing technique consists of surrounding the tuna school with a purse-seine net either on a Free Swimming School (FSC) or on a school aggregated under a floating object, called a Drifting Fish Aggregating Device (DFAD; Fonteneau et al., 2013). This technique may negatively impact biodiversity (Dagorn et al., 2013).

Although tuna purse-seine fisheries have been shown to be more selective than other fisheries (Alverson et al., 1994), several species, including vulnerable and sensitive species can be incidentally caught (e.g. Amandè et al., 2010). Many reports and other grey literature sources have already implied that the purse-seine fishery has few interactions with marine turtles in three major oceans (see review in Hall and Roman, 2013). However with low observer coverage and encounters usually less than 1 percent of sets, it is difficult to produce solid estimates of sea turtle mortality that can be attributed to the purse-seine fishery (Sánchez et al., 2007; Hall and Roman, 2013). In fact, marine turtle bycatch may appear to be a rare event in most fisheries because marine turtles do not follow the assumptions most commonly used that discards are proportional to catch or to effort, and depend on environmental conditions and fishing methods (Rochet and Trenkel, 2005; Amandè et al., 2012). Such environmental dependence is particularly noticeable in the case of interaction between marine turtles and the purse-seine fishery because of (1) the oceanic range of purse-seine fishing operation (IOTC-SC15, 2012), (2) the complex life cycle of marine turtles (Miller, 1997), (3) their great migratory capability (Luschi, 2013), and (4) the lack of knowledge about the pelagic phases of those species.

In order to identify the key issues related to purse-seine fishery interaction with marine turtles, the present paper focuses on the description of interactions between marine turtles and the European purse-seine fishery in the Atlantic and Indian oceans using 15 years of data from at-sea Spanish and French observer programs.

2. Materials and methods

2.1. Datasets

Under the European Data Collection Regulations (Council Regulation no. 1543/2000, Commission Regulation no. 1581/2004, Council Regulation no. 199/2008, and Commission Decision 2008/949/EC), the European Union established a mandatory sampling program to estimate the amount of bycatch and discards in the European Union fisheries. The French (Institut de Recherche pour le Développement – IRD) and Spanish (AZTI Tecnalia and Instituto Español de Oceanografía – IEO) research institutes collaborated to implement a common framework for collecting and analysing the data from observer programs conducted on the tropical tuna purse-seine fisheries operating in the Atlantic and Indian oceans. The observers were opportunistically placed onboard purse seiners vessels in order to cover equally the four quarters of fishing activity. The observers collected information of fishing activities, target species catches, amount of bycatches by species and size frequencies of bycatches. The information collected by observers is introduced in a common database from which the data presented in this paper were extracted (e.g. Chavance et al., 2012; for more details contact authors). Spain and France started their cooperative observer programs in 2003 and in 2005 respectively. Moreover, data from other past observer programs implemented by each country and based on the same methodology were also included in the database and analysed here (Table 1).

Although observer programs before the implementation of European Union Data Collection Regulation were slightly different, these historical programs were all conducted under the International Commission for the Conservation of Atlantic Tunas (ICCAT) aegis or within European project (Table 1). Observation protocols were developed focusing on the same objective (*i.e.* estimation of bycatch) and were implemented simultaneously by the different institutes. Data from these different programs were then aggregated. Pianet et al. (2000) showed that Spanish and French purse-seiner use similar technology and have similar fishing strategy. Catches by species and by size category are not different between countries when fishing in the same strata defined by large statistical areas, quarters and fishing modes (free school set vs. Fish Aggregating Device sets). Therefore, we assume that there are no significant differences in the level of interaction with marine turtles between both fleets and between vessels. Finally, as both countries share the same observer programs and observer training technics since their implementation, we assume that errors due to the numerous different observers were similar from both French and Spanish observer programs.

Moreover, French and Spanish Purse-seine fishing activities (FSC vs. DFADs) made available 100% coverage of logbook databases for this study and for all years analysed.

2.2. Data collection

Data are collected by observers on an exact position basis (latitude and longitude) and aggregated for the analysis by 1° statistical square when needed. Observers collected the data during observer trips when a fishing set is carried out and when a drifting object is visited. Observations on sets give information on turtle bycatch during a set on Free Swimming School (FSC) or Drifting

Table 1
Periods where French and Spanish observer programs were actives and from which database the data were extracted for this study.

Observer programs	France		Spain	
	Period	Institute involved	Period	Institute involved
Associated Fauna	1995–1996	IRD[a]	1995	IEO
ICCAT[b] Bigeye Year	1998–1999	IRD	1997–1999	IEO
ICCAT Moratorium	1997–2005	IRD		IEO
EU DCR[c]	2005–2011	IRD	2003–2011	AZTI[e] and IEO[f]
TAAF[d]	2009–2011	TAAF and IRD	–	–

[a] Institut de Recherche pour le Développement.
[b] The International Commission for the Conservation of Atlantic Tunas.
[c] European Union Data Collection Framework.
[d] Terres Australes et Antarctiques Françaises.
[e] Tecnalian Unidad de Investigación Marina.
[f] Instituto Español de Oceanografía.

Fish Aggregating Device (DFAD). Observations on drifting object, without associated fishing set, can also occur when the object is just visited. During a visit, the object can be hauled onboard or not. In the latter case the entanglement of turtles in the deeper part of the net hanging underneath the DFAD cannot be annotated by the observer. Filmalter et al. (2013) did 51 diving observations under DFAD in the Indian Ocean and estimated significant sharks entanglement in the lower part of DFADS. However, during these observations, Forget (comm. pers) counted two turtles entangled on the superior part of the DFAD and therefore not hidden from observers, but does not find any turtle entangled underneath DFADs.

As drifting objects are not individually identified and as their position can change, one object can be observed several times. The observer takes note of the presence, absence and/or entanglement of any animal, including turtles and their fate. Data from observed purse-seine sets range from 1995 to 2011 whereas data from object observations range from 2003 to 2011.

When marine turtle bycatch occurs, observers reported the exact date, GPS position and numbers of individuals by species. Species identification remains a key issue for validation in the database. Observers have specific training before going at sea that includes marine turtle species identification. When a doubt occurs while onboard, observers take various photos for cross validation by experts. Marine turtles were not systematically measured. For the one measured (Carapace Curved Length – CCL), it was possible to assess the maturity stage according to species size-at-maturity data available in the literature. If the size was below maturity, we considered that the individual was a juvenile. Finally, observers also noted the fate of the turtle (alive or dead) when returned to the sea.

Before analysing the dataset, a quality control procedure was applied to the datasets to check inconsistencies when data were entered in the database. Doubtful data which could not be corrected were discarded from the database, such as incorrect 1° statistical squares, isolated typos and duplicated observations. Marine turtle data (*i.e.* species, location, size...) were also checked one by one and compared to the literature to identify any inconsistency with known species biology such as maximum size and distribution. In such cases, the observation was corrected if possible or eliminated.

2.3. Analysis and mapping

Data were categorized using two fishing modes (DFAD or FSC) that are known to explain most of variability in bycatch in purse-seine fishery (Delgado de Molina et al., 2000; Romanov, 2002; Sánchez et al., 2007; Amandè et al., 2010). However, analyses were performed for ocean basins because (1) marine turtle are identified in separate Regional Management Units in both oceans (Wallace et al., 2011), (2) there is currently little information showing any connectivity between marine turtle stocks in the Atlantic and Indian oceans (e.g. for green turtle, see Bourjea et al., 2007) and (3) the spatial distribution of catch and effort from European purse-seine in both oceans are very different (e.g. IOTC-SC15, 2012). In order to assess a spatial and temporal effect on marine turtle bycatch, observed data were stratified per 1° statistical square, year and quarters. Whenever possible, analyses per species composition and maturity stage were also spatially conducted.

In order to avoid bias from the observation effort, we weighted marine turtle observations to the total observation effort. To obtain the number of observed turtles per observed set or per observed object per year, we worked at the 1° statistical square and divided the total number of observed turtles by the total observed sets or object observed per year. The annual mean of observed turtles per observed set or object and respective standard deviation were then calculated per ocean and per fishing mode.

To observe the spatial distribution of marine turtle bycatch by species, the latitudinal and longitudinal barycentres of turtle bycatch or observed turtles on object were calculated yearly for each species in both oceans. GPS positions of bycatch were used to estimate the Utilisation Distribution of interaction (UD) with the kernels method (Worton, 1989, 1995). The Utilization Distribution is the bivariate function giving the probability density of the animal to be found at a point according to its known geographical coordinates. Using this method, a home range can be estimated as the minimum area in which an animal has some specified probability of being located. The functions we used here correspond to the approach described in Worton (1995) and implemented using R (adehabitat and maps packages). All maps were drawn using Arcgis 10.2 and statistics analyses were performed using R software (R Core Team, 2013).

2.4. Data extrapolation

We carried out a tentative extrapolation of the observed bycatch data to the total fishing effort per year and oceanic region in order to have an order of magnitude of the total number of marine turtles incidentally caught by the purse-seine fishery in the Atlantic and Indian oceans. We used information derived from French and Spanish fishing statistics logbooks to determine a raising factor based on the effort of the fleets (number of sets on FSC and DFAD per 1° square and per year). In this way, we established an estimation of the total marine turtle bycatch based on information during observed sets. Since there is no available information on the total number of DFAD deployed by the European purse-seine fishery, it was not possible to raise the data to the total number of DFADS to estimate the real impact on turtle's interaction with drifting DFAD.

3. Results

3.1. European purse-seine fishing and observation efforts

From 1995 to 2011, more than 213 000 sets were undertaken by the European purse-seine fleets in both the Atlantic and Indian oceans and reported in logbooks (Tables 1 and 2). A total of 15 913 purse-seine sets on DFAD and FSC from 1995 to 2011 and 14 123 drifting objects from 2003 to 2011 were observed by onboard observers (Tables 1 and 2). The average yearly observer coverage of the purse-seine nets was significant with 10.0% (SD = 7.9) in the Atlantic and 8.9.3% (SD = 9.1) in the Indian ocean of the purse-seine sets observed over this period (Table 2).

As the observers were placed onboard fishing vessels to cover equally the 4th quarters of fishing activity, we assumed that observer sets are representative of the total fleet effort. In fact, observed sets distribution overlap with fishing sets distribution (Figs. 1A and B and 2A and B); which support this assumption. The coverage of fishing set observation varied greatly from 1995 to 2011 in both oceans and between and within the observed fishing mode (Table 2). For instance, the sampling coverage between oceans is different in 2010, with an Atlantic coverage (11.4%) higher than that of the Indian Ocean (8.3%). Similarly, there is different coverage between fishing modes in 2010, with sets on FSC being more extensively covered (10.6%) than sets on DFAD (7.6%; Table 2). Besides, the level of total sets on FSC is almost the same in the Atlantic (50 914 sets) and Indian (52 531 sets) oceans (Table 2), but double the observed sets were carried out on FSC in the Atlantic, due to the fact that European purse-seine fishery used to fish twice as much on DFAD in the Indian Ocean (61 734 sets) than

Table 2
Number of purse-seine sets, observed sets, observed floating objects and observed marine turtles bycatch per year for the French and Spanish Purse seine fleet in the Atlantic and Indian oceans. DFAD: Drifting Fish Aggregating Device; FSC: Free Swimming School; SD: Standard Deviation; nb: number.

Year	Fishing sets												Object	
	DFAD					FSC					Unkown		nb object observed	nb Of marine turtle bycatch
	Total sets	Observed sets	Coverage (%)	nb Of marine turtle bycatch	Annual bycatch rate	Total sets	Observed sets	Coverage (%)	nb Of marine turtle bycatch	Annual bycatch rate	Total sets	Observed sets		
Atlantic Ocean														
1995	3690	71	1.9	5	0.070	4754	249	5.2	15	0.060	156	0		
1996	3466	1	0		0.000	4330	39	0.9	1	0.026	38	0		
1997	2412	259	10.7	14	0.054	3717	774	20.8	28	0.036	109	0		
1998	2153	715	33.2	54	0.076	4371	1585	36.3	43	0.027	326	0		
1999	1782	404	22.7	26	0.064	3576	737	20.6	18	0.024	237	0		
2000	2144	104	4.9	1	0.010	3686	237	6.4	9	0.038	196	0		
2001	2055	151	7.3	1	0.007	3698	397	10.7	4	0.010	191	0		
2002	1643	136	8.3	2	0.015	3103	220	7.1	3	0.014	82	0		
2003	1910	198	10.4	13	0.066	4148	357	8.6	16	0.045	57	0	121	0
2004	1921	184	9.6	3	0.016	2562	233	9.1	3	0.013	91	0	121	2
2005	1429	86	6	5	0.058	1976	112	5.7	4	0.036	28	0	162	1
2006	1231	31	2.5	1	0.032	1505	66	4.4	4	0.061	12	0	168	0
2007	1449	82	5.7	4	0.049	1519	107	7	7	0.065	8	0	341	13
2008	2030	177	8.7	7	0.040	2063	217	10.5	9	0.041	8	0	504	15
2009	2710	163	6	8	0.049	2994	261	8.7	12	0.046	2	0	583	22
2010	3702	326	8.8	34	0.104	2912	432	14.8	23	0.053	12	0	1421	32
2011	3280	295	9.0	23	0.078	1594	362	22.7	15	0.041	0		1354	31
1995–2011	39,007	3383	9.2 (SD = 7.9)	201	0.046 (SD = 0.029)	52,508	6023	11.7 (SD = 8.8)	214	0.037 (SD = 0.017)	1553	0	4775	116
Average per observation				0.059					0.036					
Indian Ocean														
1995	2275	65	2.9	8	0.123	2247	365	16.2	16	0.044				
1996	1998					1953								
1997	2247					1364								
1998	1998	486	24.3	24	0.049	1332	680	51.1	4	0.006				
1999	1617					1622								
2000	5076					3669					189	0		
2001	4281					4278					176	0		
2002	5103					3107					108	0		
2003	3883	108	2.8	6	0.056	4136	64	1.5	1	0.016	149	0	331	4
2004	3449	146	4.2	8	0.055	4927	94	1.9		0.000	127	0	864	3
2005	4443	166	3.7	5	0.030	5635	298	5.3	3	0.010	176	0	596	3
2006	5295	294	5.6	21	0.071	5635	248	4.4		0.000	49	0	790	28
2007	5114	411	8	41	0.100	4676	464	9.9	5	0.011	3	0	1822	89
2008	4748	442	9.3	18	0.041	4236	256	6	1	0.004	11	0	1434	59
2009	4940	461	9.3	6	0.013	1989	189	9.5		0.000	4	0	1732	21
2010	5267	401	7.6	9	0.022	1725	182	10.6	1	0.005	8	0	1071	15
2011	5320	152	2.9	2	0.013	2050	173	8.4	3	0.017	0		708	16
1995–2011	67,054	3132	7.8. (SD = 6.2)	148	0.052 (SD = 0.035)	54,581	3013	11.3 (SD = 13.9)	34	0.01 (SD = 0.013)	1000	0	9348	238
Average per observation				0.047					0.011					0.025

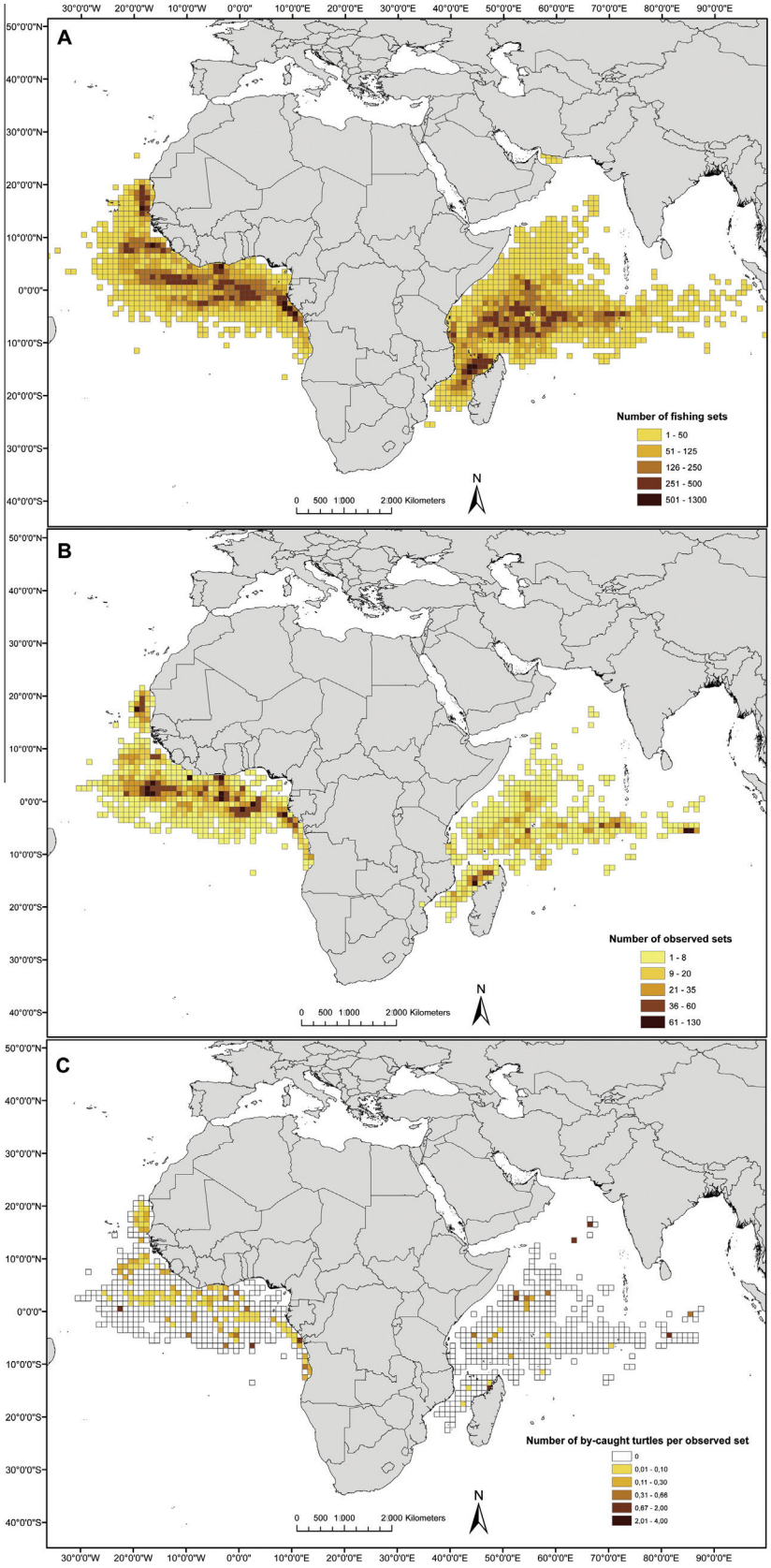

Fig. 1. Total number of purse-seine sets on FSC (A), observed sets on FSC (B) and number of marine turtles bycatch per observed set on FSC (C) per statistical square of 1° in the French and Spanish Purse seine fleet from 1995 to 2011 in the Atlantic and Indian oceans.

in the Atlantic Ocean (35 727 sets; Table 2). This difference in fishing strategy on DFAD between oceans is not taken into account in the observation effort since there are around 3000 set observations on FAD in both oceans (Table 2).

The comparison of the spatial and temporal distribution between purse-seine sets and observed sets was already discussed in Amandè et al. (2008, 2012; see also Supplement material for temporal distribution of effort and observer coverage); thus, we provide here only the global picture of those distributions. The spatial coverage of the observer programs in term of sets on FSC seems to contribute good coverage of the whole fishing area and effort (Fig. 1A and B and Supplement material). The coverage for DFAD is well distributed in the Atlantic Ocean, but in the Indian Ocean, we noted that the Mozambique Channel is over represented compared to the North-Western Indian Ocean (Fig. 2A and B). Per quarter, the observation coverage seems also to not detect any significant discrepancies with the fishing area and effort in both oceans (see Supplement material). In the Indian Ocean, the fishing effort is concentrated in the Mozambique Channel during the end of the first and all the second quarters, before moving to the north western in the third, fourth and beginning of the first quarters. In the Atlantic Ocean, the fishing effort does not display any strong spatial pattern along the year.

In addition to the observed fishing sets, more than 14 000 drifting objects were also directly observed in both oceans from 2003 to 2011 (66% in the Indian Ocean; 34% in the Atlantic Ocean; Table 2). By comparing the fishing effort on DFAD to the observation of drifting objects (Figs. 2A and 3A), the object observation effort seems to adequacy cover the total fishing effort on DFAD in Atlantic Ocean, but in the Indian Ocean the north Mozambique Channel remains again over observed.

3.2. European purse-seine marine turtle bycatch on observed sets

Out of the 15 913 sets observed from 1995 to 2011, 597 marine turtles were accidentally caught, 415 and 182 in the Atlantic and Indian oceans respectively (Table 2). Even if the average annual number of bycatch per number of observed sets in the Atlantic (0.04, SD = 0.02) and Indian (0.03, SD = 0.02) oceans is similar (*t*-test, $p > 0.05$), there is a significant difference in the number of bycatch according to the fishing mode, only in the Indian Ocean, with an annual average number bycatch per observed sets on FSC smaller () than on DFAD (0.05, SD = 0.04 and 0.1, SD = 0.01 respectively; *t*-test, $p < 0.001$).

More than 76% of the turtles were identified and 93% were allocated a fate (Table 3). Upon the 597 turtles accidentally caught, 91% and 77% were released alive in the Atlantic and Indian oceans respectively, which represents 21 and 20 dead turtles observed in the Atlantic and Indian oceans, respectively, over the period (Table 3). In both oceans, the percentage of marine turtles returned to the sea alive is very similar between DFAD and FSC (respectively 92.0% and 89.3% in the Atlantic Ocean, and 76.4% and 79.4% in Indian Ocean). *Lepidochelys* sp., both Kemp's Ridley and olive are the most frequently encountered in both oceans with 172 observations; followed by loggerhead (*Caretta caretta*; $N = 73$) and leatherback (*Dermochelys coriacea*; $N = 67$) turtles in the Atlantic Ocean whereas in the Indian Ocean they are followed by hawksbill (*Eretmochelys imbricata*; $N = 37$) and green turtles (*Chelonia mydas*; $N = 32$). Bycatch of leatherback turtles remains rare in the Indian Ocean with only two observations from 1995 to 2011.

The size and the life stage were determined for 352 of the marine turtles, with 68% estimated to be adults in the Atlantic while most turtles were juvenile in the Indian Ocean (74%; Table 4).

3.3. European purse-seine marine turtle bycatch on observed floating objects

From 2003 to 2011, 354 marine turtles were recorded on 14 124 floating objects, 116 of which were in the Atlantic Ocean and 238 in the Indian Ocean (Table 2). The mean number of observed turtles per object per year is very similar in the Atlantic Ocean (0.019, SD = 0.015) and the Indian Ocean (0.022, SD = 0.016); which is lower than the mean number of marine turtles observed per set and year (Table 2).

Of the observed marine turtles on floating objects, 74% were identified. In the Indian Ocean, the species composition is very similar to the one observed on purse-seine sets: the dominant species is olive Ridley (*Lepidochelys olivacea*; $N = 74$), followed by the hawksbill ($N = 40$) and the green turtle ($N = 37$) (Table 5). As for fishing set observations, occurrence of leatherback turtle is rare ($N = 6$). In the Atlantic Ocean, the most observed turtles are again the two species of *Lepidochelys* (41 olive Ridley and 12 Kemp's Ridley turtles). No difference was observed between the 4 other species that are rarely caught (<8). Most of the turtles observed at a floating device were alive whilst still entangled or already free. Hence, 93% and 73% of the individuals were released alive in the Atlantic and Indian oceans respectively, which is similar to the values found on purse-seine sets for both oceans (Tables 5).

3.4. Spatial distribution of marine turtle bycatch on observed sets

Over the study period and in both oceans, the areas where interactions between European purse-seine and marine turtles occur cover the entire fishing zones (Fig. 4A and B, see also Supplement material for temporal effect), and are illustrated by the estimated utilisation distribution of observed bycatch using a kernel approach (Fig. 5A). This approach allows us to suggest that, even if interaction occurs in all the fishing area in the Atlantic Ocean, there are clearly defined hotspots of interactions in the Indian Ocean, e.g. off the coast of Somalia and in the northwest Madagascar. Due to the low number of interaction, and the number of species of marine turtle that interact with this fishery, temporal distribution of marine turtle bycatch over the year was not investigated (see Supplement material for maps per quarter).

In order to assess a spatial pattern per species, we plotted the barycentres of the turtle bycatch for each species in both oceans (Fig. 5A). In the Atlantic Ocean, the distributions do not show any specific spatial pattern. The olive Ridley ($N = 76$) and Kemp's Ridley ($N = 37$) turtles are accidentally captured in the eastern area of the fishing zone while leatherback ($N = 67$), loggerhead ($N = 73$) and green ($N = 40$) turtles are mainly found in the western area. In the Indian Ocean, although there are also large standard deviations, both in longitudes and latitudes, a clearer spatial distribution by species in relation to fishing activity is observed. The olive Ridley ($N = 58$) is clearly found more in the northern area while hawksbill ($N = 37$) and green ($N = 32$) turtles are found more in the southern part of the fishing area. These two species are also the only ones observed in the Mozambique Channel (Fig. 4). The loggerhead turtle ($N = 19$) is distributed mainly in the northern area which in the Indian Ocean is limited between the Mozambique Channel and Somalia. Such observations are highlighted in distribution estimations using the Kernel approach in both oceans by species.

Bycatch of marine turtles per unit of observation effort (*i.e.* observed sets) from 1995 to 2011 are shown in Figs. 1C and 2C. The mean number of by-caught turtles per observed sets was very low in both DFAD and FSC sets (<0.044 turtles; SD < 0.029) in the Atlantic and Indian oceans (<0.056 turtles; SD < 0.034), meaning that most of the time, captures per set rarely account to more than a single individual (Table 6). The highest capture rates on DFAD and FSC occur in the North Western Indian Ocean but are low in

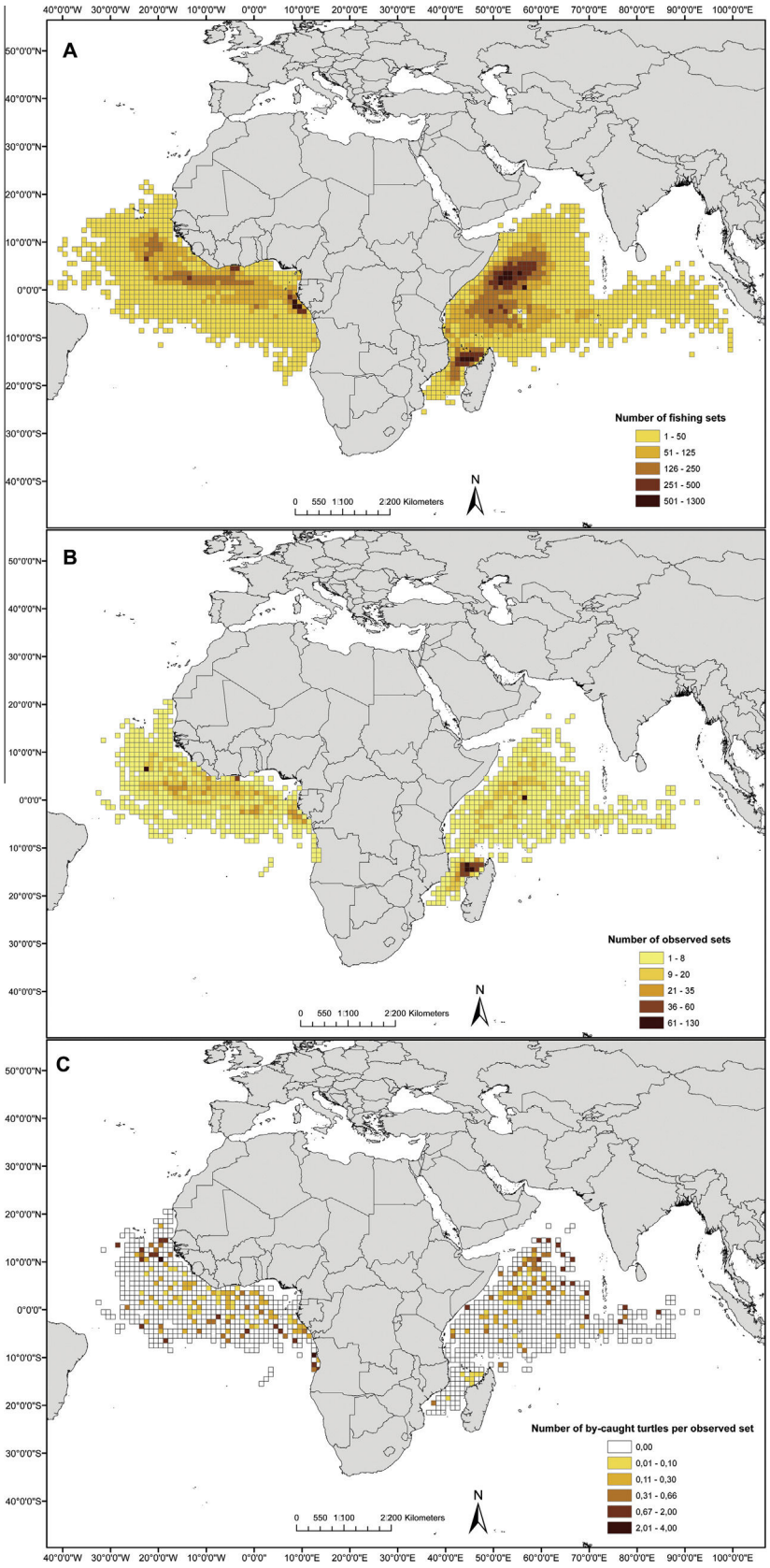

Fig. 2. Total number of purse-seine sets on DFADs (A), observed sets on DFADs (B) and number of marine turtle bycatch per observed set on DFADs (C) per statistical square of 1° in the French and Spanish Purse seine fleet from 1995 to 2011 in the Atlantic and Indian oceans.

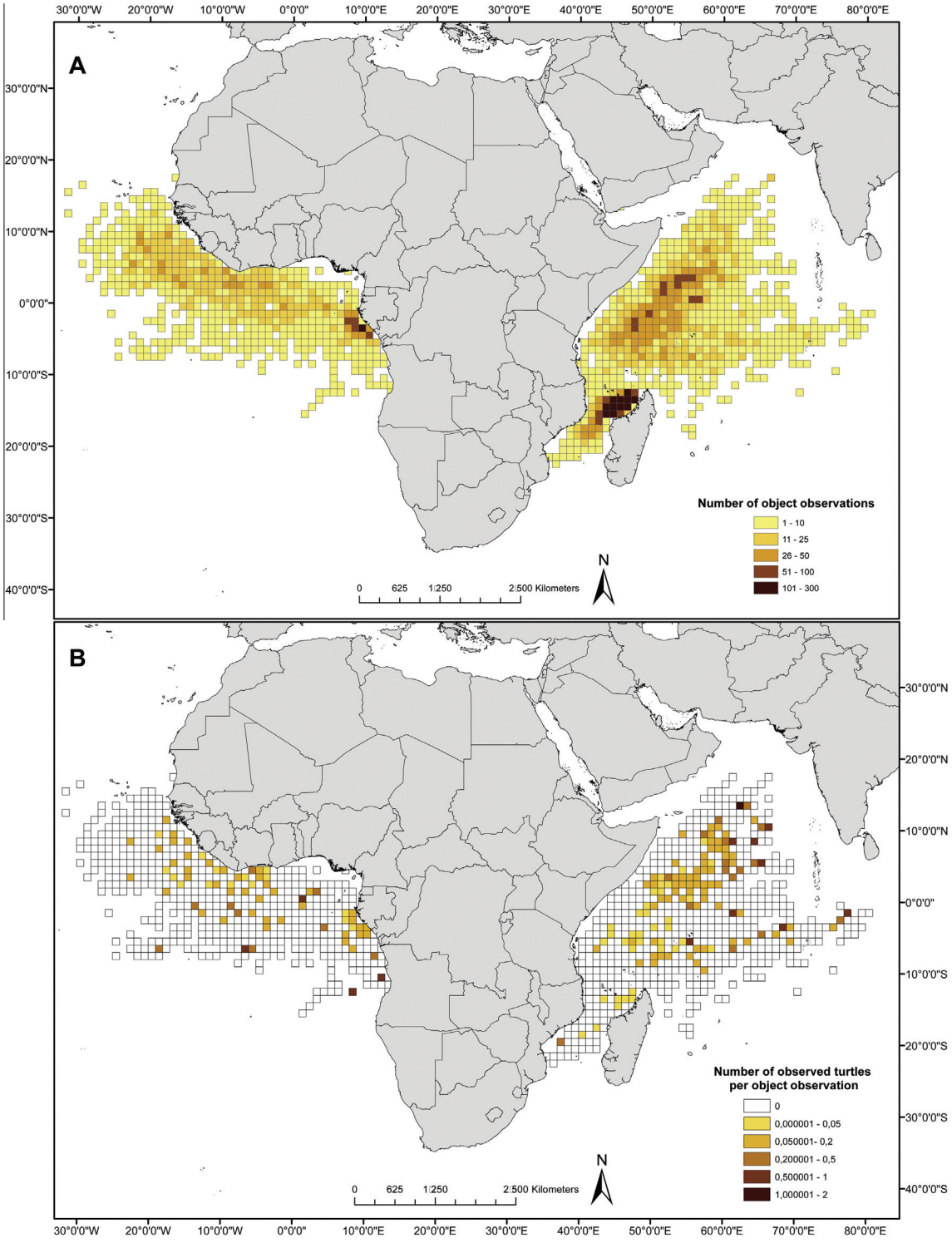

Fig. 3. Total number of object observed (A) and number of observed marine turtles per object observation (B) per statistical square of 1° in the French and Spanish Purse seine fleet from 2003 to 2011 in the Atlantic and Indian oceans.

the Mozambique Channel even with a higher observation effort. In the Atlantic, accidental captures occur more or less in all the fishing areas with a high level of bycatch per unit of observed effort off the Guinea coast.

3.5. Spatial distribution of marine turtle bycatch on observed objects

As for observation on purse-seine sets, marine turtles interacted with floating objects in the whole Atlantic and Indian oceans fishing area (Figs. 3A and 5B). In the Indian Ocean, we observed the same pattern as for set observations, with the highest turtle observation rates located in the Northern area (Somali basin) while no specific pattern was observed in the Atlantic (Fig. 3B).

We also plotted barycentres of the observed turtles for each species in both oceans (Fig. 5B) and we found a similar pattern as observed for purse-seine sets: the distributions of different turtle bycatch almost completely overlap in the Atlantic with the olive ($N = 41$) and Kemp's Ridley ($N = 12$) being observed more towards

Table 3
Total number of marine turtle bycatch in observed purse-seine sets of French and Spanish Purse seine fleet in the Atlantic and Indian oceans. Numbers are provided by ocean, species, fate (alive/dead) and percentage of turtles released alive and dead by fishing mode. DFAD: Drifting Fish Aggregating Device; FSC: Free Swimming School.

Species			Atlantic Ocean				Indian Ocean				Total
Scientific name	Common name	Code	Alive	Dead	Unknown	Total	Alive	Dead	Unknown	Total	
Caretta caretta	Loggerhead	CCC	67	3	3	73	13	3	3	19	92
Chelonia mydas	Green turtle	CMM	36		4	40	24	2	6	32	72
Dermochelys coriacea	Leatherback	DCC	60	4	3	67	2			2	69
Eretmochelys imbricata	Hawksbill	EIM	12	2		14	32	2	3	37	51
Lepidochelys kempii	Kemp' turtle	LKE	35	2	1	38					38
Lepidochelys olivacea	Olive ridley	LCE	73	1	2	76	47	4	7	58	134
Unidentified turtles	–	–	93	9	5	107	22	9	3	34	141
		Total	376	21	18	415	140	20	22	182	
		Occurrence (%)	91	5	4		77	11	12		
		On DFAD	185	7	9	201	113	16	19	148	597
		Occurrence (%)	92.0	3.5	4.5	48.4	76.4	10.8	12.8	81.3%	
		On FSC	191	14	9	214	27	4	3	34	
		Occurrence (%)	89.3	6.5	4.2	51.6	79.4	11.8	8.8	18.7%	

Table 4
Total number of marine turtle bycatch in observed purse-seine sets of French and Spanish Purse seine fleet in the Atlantic and Indian oceans. Numbers are provided by ocean, species and life stage (adult/juvenile) and percentage of identified adult and juvenile turtles by ocean.

Species	Atlantic Ocean				Indian Ocean				Total
	Adult	Juvenile	Unknown	Total	Adult	Juvenile	Unknown	Total	
Caretta caretta	21	7		28	1	9	2	12	40
Chelonia mydas	5	18		23	3	18	1	22	45
Dermochelys coriacea	47	16		63					63
Eretmochelys imbricata	2	6		8		31		31	39
Lepidochelys kempii	34	9		43					43
Lepidochelys olivacea	48	16		64	17	27		44	108
Unidentified turtles	2	2	2	6		2	6	8	14
Total	159	74	2	235	21	87	9	117	352
Occurrence (%)	68	31	1		18	74	8		

Table 5
Total number of marine turtles observed at floating objects by species and fate (alive/dead) in the Atlantic and Indian oceans.

Species	Atlantic Ocean				Indian Ocean				Total
	Entangled alive	Entangled dead	Free	Total	Entangled alive	Entangled dead	Free	Total	
Caretta caretta	6		1	7	10	6	2	18	25
Chelonia mydas	2		4	6	12	10	15	37	43
Dermochelys coriacea	4		4	8	2		4	6	14
Eretmochelys imbricata	4		2	6	17	10	13	40	46
Lepidochelys kempii	2		10	12					12
Lepidochelys olivacea	26	1	14	41	34	21	19	74	115
Unidentified turtles	14	7	15	36	34	18	11	63	95
Total	58	8	50	116	109	65	64	238	350
Occurrence (%)	50	7	43		46	27	27		

the eastern area (Fig. 5B). However, the hawksbill distribution ($N = 6$) is located in the northern fishing area and seems to be less dispersed than the other species (CCC = 7, CMM = 6, DCC = 8, LKE = 12 and LOL = 41). In the Indian Ocean the same pattern as for sets was observed, with hawksbill ($N = 40$) and green ($N = 37$) turtles more often observed in the southern area while the olive Ridley ($N = 74$) observations on objects were located more towards the Northern Indian Ocean. Loggerhead ($N = 18$) and leatherback ($N = 6$) turtles were observed in northern latitudes.

3.6. Total EU marine turtle bycatch estimation

Using the number of accidentally captured marine turtles per observed sets by year, by fishing mode and the total fishing effort in number of sets available for the European purse-seine in both oceans, an estimation was produced of the order of magnitude of the total number of marine turtles interacting with the European purse-seine fishery (Table 6). The total incidental capture of marine turtles was estimated at 3 849 individuals in the Atlantic Ocean over the period from 1995 to 2010 and 2 581 in the Indian Ocean for 2003–2011. Based on marine turtle survival rate estimated using observed data on purse seine sets, we estimated that 222 and 390 marine turtles died in the Atlantic and Indian oceans respectively over those 17 and 9 years periods respectively (Table 3). On average, we found that the annual European purse-seine bycatch rate for marine turtles was 226 (SD = 148) and 235 (SD = 153) in the Atlantic and Indian oceans respectively, which corresponds to an estimated average annual death of 13 (SD = 22) and 35 (SD = 39) marine turtles in the Atlantic and Indian oceans. Even with a large standard deviation due to the low observation rate, it is estimated that this fishery kills less than 50 marine turtles per year for both oceans combined.

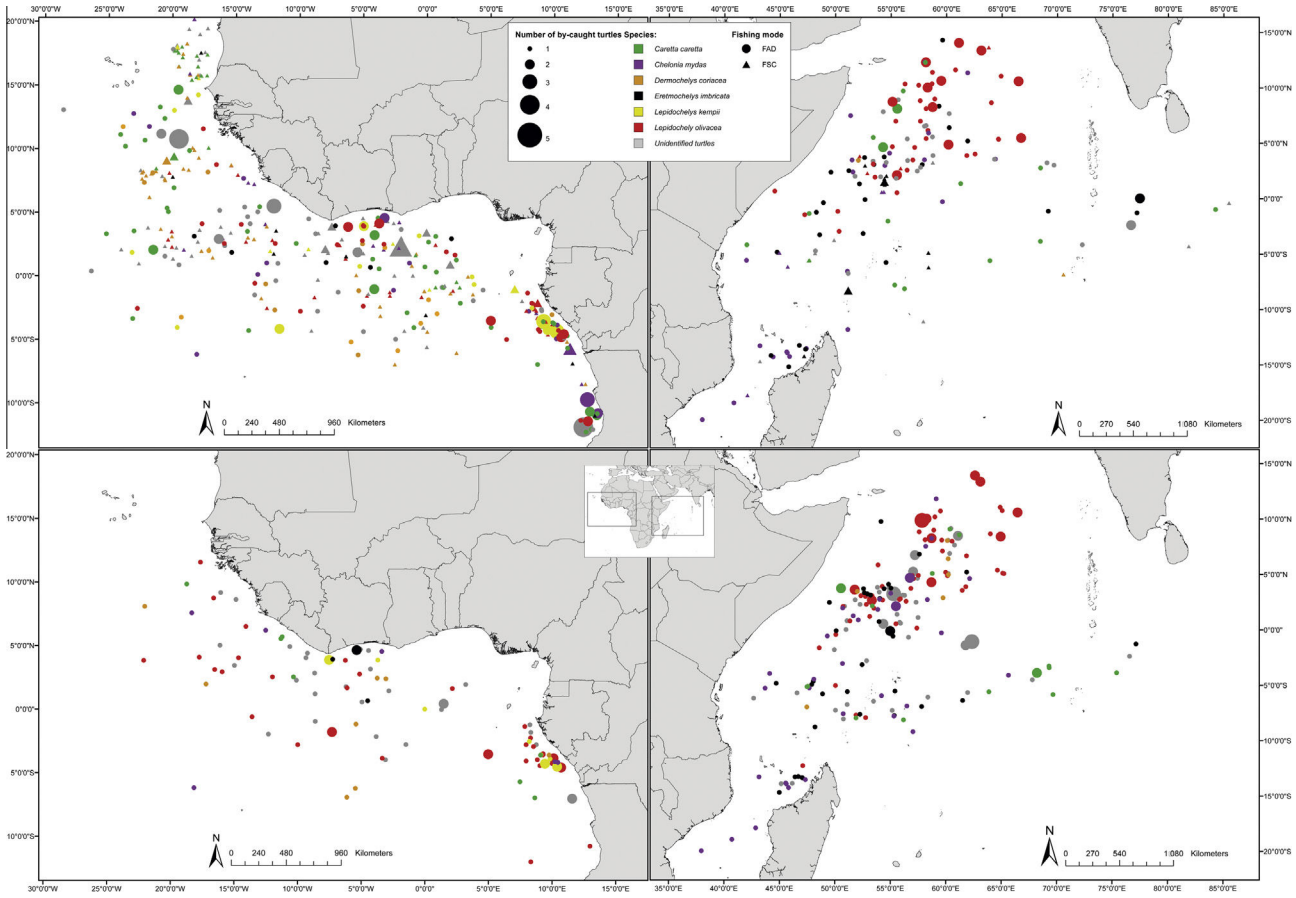

Fig. 4. Distribution of observed marine turtles bycatch by species in the French and Spanish Purse seine fishing on FADs and FSCs sets in the Atlantic (A) and Indian (B) Oceans for the period 1995–2011. Observed marine turtles on floating devices during the study period 2003–2011 are also presented for the Atlantic (C) and Indian (C) Oceans.

4. Discussion

4.1. Global marine turtle bycatch assessment in European purse-seine fishery

Based on data from observer programs and logbook data from 1995 to 2011, this study presents an attempt to evaluate the global bycatch on marine turtles of the European Union oceanic purse-seine fishery operating in the Atlantic and Indian oceans.

Observations were carried out using a significant number of purse-seine sets with observers (15 913 sets) and direct observations on floating objects (14 123 objects) used by this fleet to catch tuna and tuna-like species. The average annual observed sets is quite an important sample of the fishing activity for such an industrial fishery (Atlantic Ocean: 10.0% (SD = 7.9); Indian Ocean: 9.3% (SD = 9.4) (Table 2)) even if it is still below the optimal level necessary for an accurate estimation of the total bycatch (Hall and Roman, 2013). Amandè et al. (2008, 2012) showed that the current sampling coverage in the observer programs of the European purse-seine fishery resulted in large uncertainties in precision and accuracy of bycatch estimates by species. As marine turtle bycatch was reported to be rare events (Sims et al., 2008; Amandè et al., 2012), the coverage rate should even be higher to allow a good estimation of the impact on these endangered species. For instance, in the case of whales, the required observer coverage is 100% for the Atlantic shark gillnet fishery, during those times of the year when whales are calving (NMFS, 2002). In the Pacific Ocean, purse-seine observer programs have covered 20–100% of the fishing effort (Lennert-Cody et al., 2004; Hall and Roman, 2013). The coverage levels of at least 50% of total effort for rare species would give reasonably good estimates of total bycatch of rare species (see review in Babcock et al., 2003). These observation levels would be ideal to obtain a good estimate of bycatch levels, but however, are costly, given the availability of resources and economic or logistic constraints that allow only low sampling of the activity (Hall, 1999). Alternative ways to improve onboard surveillance should be investigated, such as electronic monitoring, which may make it possible to implement cost effective programmes and to increase observation coverage.

Despite uncertainties revealed by large standard deviations due to the rarity and highly variable events (1–5 turtles/set) and low sampling rates, we estimated that an average annual of 218 (SD = 150) and 249 (SD = 153) marine turtles were recorded as bycatch by the European purse-seine fishery in the Atlantic and Indian oceans respectively. This level of bycatch from European purse-seine remains very low in comparison to other open sea industrial fishery gears commonly used in both oceans: longline fishery that results in a substantial level of marine turtle bycatch (see review in Read, 2007; e.g. Lewison et al., 2004; Petersen et al., 2009), gillnet (e.g. Benhardouzea et al., 2012) or bottom trawl fishery (e.g. Fennessy et al., 2008). For example, Casale (2011) estimated that 39 000 marine turtles are captured per year by the bottom trawl fleet in the Mediterranean and 23 000 marine turtles are recorded as bycatch annually in the set nets fleet in the Mediterranean.

It has been demonstrated that the survival rates of marine turtle after an interaction with European purse-seine fishery are high, 0.95 (SD = 0.09) and 0.87 (SD = 0.15) in the Atlantic and Indian oceans, respectively, which can be compared with an estimation of 13 (SD = 22) and 37 (SD = 40) individual deaths on average per

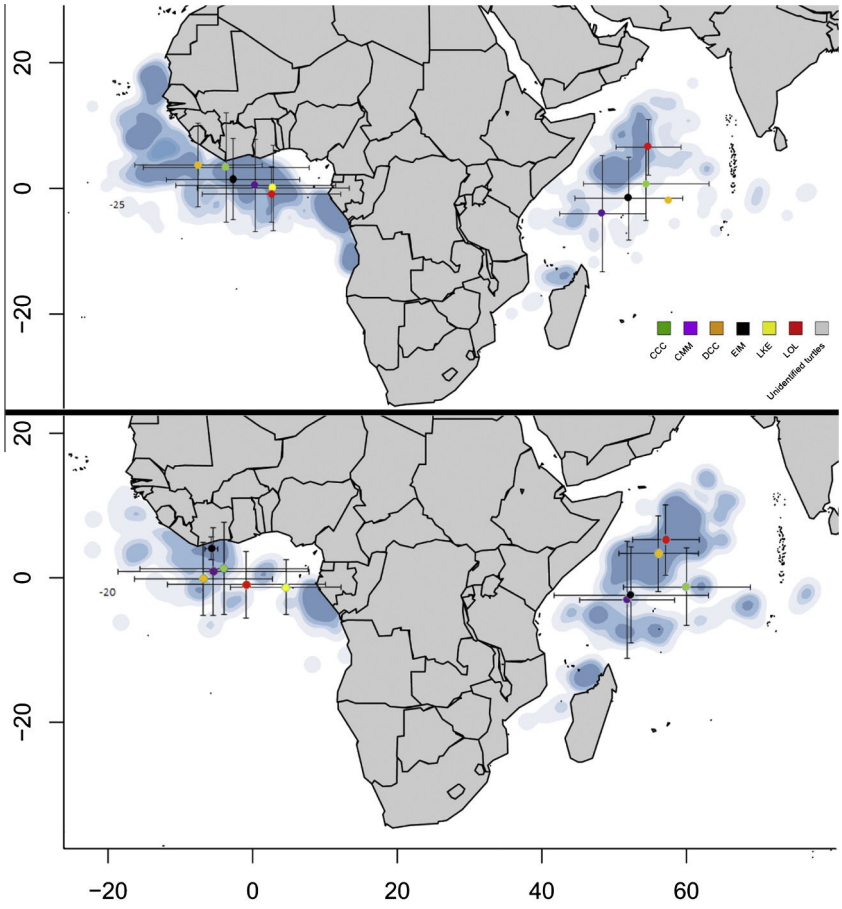

Fig. 5. Estimated utilization distributions with the kernel method using marine turtle geographical interactions with European purse-seine. Data used are from observed purse-seine sets for the period 1995–2011 (A) and from observed floating devices during the study period 2003–2011 (B). Both (A) and (B) also show latitudinal and longitudinal barycentres and standard deviations of each species captured by European purse-seine fleet during observed sets (A) and observed on floating objects (B). (A) CCC: *Caretta caretta* (Atlantic Ocean $N = 73$; Indian Ocean $N = 19$), CMM: *Chelonia mydas* (Atlantic Ocean $N = 40$; Indian Ocean $N = 32$), DCC: *Dermochelys coriacea* (Atlantic Ocean $N = 67$; Indian Ocean $N = 2$), EIM: *Eretmochelys imbricata* (Atlantic Ocean $N = 14$; Indian Ocean $N = 37$), LKE: *Lepidochelys kempii* (Atlantic Ocean $N = 37$) and LOL: *Lepidochelys olivacea* (Atlantic Ocean $N = 76$; Indian Ocean $N = 58$). (B) CCC (Atlantic Ocean $N = 7$; Indian Ocean $N = 18$), CMM (Atlantic Ocean $N = 6$; Indian Ocean $N = 37$), DCC (Atlantic Ocean $N = 8$; Indian Ocean $N = 6$), EIM (Atlantic Ocean $N = 6$; Indian Ocean $N = 40$), LKE (Atlantic Ocean $N = 10$) and LOL (Atlantic Ocean $N = 41$; Indian Ocean $N = 74$).

year in the Atlantic and Indian oceans respectively. As for comparisons, Casale (2011) estimated that turtle mortality rate in the entire Mediterranean fleet were 20%, 30%, 40% and 60% for the bottom trawl, pelagic long-line, demersal long-line and set net fisheries, respectively, leading to an estimated of annual total mortality of 44 000 turtles. Being aware that the European purse-seine fishery represents 56% and 63% of the total purse-seine catches in the Atlantic and Indian oceans respectively over the 1995–2011 period (Chassot et al., 2013; Delgado de Molina et al., 2013), our estimates tend to indicate a very low impact of European purse-seine on marine turtle populations in comparison to other industrial fisheries or, at least, that is clearly not of the same order of magnitude as other fisheries. However, it is worthwhile noting that comparing the impact on marine turtle of different fisheries is very context specific and should take into account the abundance by species of the affected population (e.g. Dalleau et al., 2014).

4.2. Comparative impact of DFAD vs. FSC

Previous dedicated studies have suggested that interactions between purse-seine and tuna-like species are mainly due to the increase attraction resulting from the netting materials used to wrap around and under the DFADs (Fonteneau et al., 2000; Sánchez et al., 2007; Amandè et al., 2008, 2010; Hall and Roman, 2013). The netting may act as protection from predators, a source of food (Gooding and Magnuson, 1967), or a meeting location (Fréon and Dagorn, 2000). The results from the present study do not support the assumption that DFAD is by far the main source of incidental captures of marine turtles in purse-seine fishery. Our findings for the Atlantic Ocean lead to the same conclusions as Hall and Roman (2013) in the Pacific Ocean, in that the mean number of by-caught turtles per observed set is very similar between fishing modes. However in the Indian Ocean, more turtles are observed when sets occur on DFADs than FSC. It seems difficult to explain such differences but also it was observed that catches of juveniles are significantly higher in the Indian Ocean (74%; $N = 87$) while bycatch was largely dominated by adults in the Atlantic Ocean (68%; $N = 159$). Witherington et al. (2012) showed that several species of young marine turtles have been observed to aggregate on Sargassum-dominated drift communities and that their diet was composed principally of Sargassum-community associates. These observations lead us to hypothesize that juvenile marine turtles in their drifting pelagic phase, may be more attracted by DFADs looking for protection, food or a rest site rather than just drifting. The differences observed between the Atlantic and Indian oceans may only be a consequence of the abundance of open sea juvenile marine turtles in the fishing area. Models of drifting trajectories of immature marine turtles have been already developed in the Atlantic Ocean (Blumenthal et al., 2009; Monzón-Argüello et al., 2010; Lohmann et al., 2012; Proietti et al., 2012). On the one hand, juveniles born along the west African coast appear

Table 6
Estimation of the total number of marine turtle bycatch in the French and Spanish Purse seine fleet in the Atlantic and Indian oceans from 1995 to 2010. DFAD: Drifting Fish Aggregating Device; FSC: Free Swimming School; SD: Standard Deviation.

Year	Number of by-caught turtles per observed set		Total number of fishing sets		Survival rate	Total estimation of by-caught turtles	Total estimation of dead turtle
	DFAD	FSC	DFAD	FSC			
Atlantic Ocean							
1995	0.07	0.06	3690	4754	0.89	544	57
1996	0.00	0.03	3466	4330	1.00	113	0
1997	0.05	0.04	2412	3717	0.72	264	74
1998	0.08	0.03	2153	4371	0.99	282	3
1999	0.06	0.02	1782	3576	1.00	200	0
2000	0.01	0.04	2144	3686	0.90	162	16
2001	0.01	0.01	2055	3698	1.00	51	0
2002	0.02	0.01	1643	3103	1.00	68	0
2003	0.07	0.05	1910	4148	0.93	313	22
2004	0.02	0.01	1921	2562	0.75	64	16
2005	0.06	0.04	1429	1976	1.00	154	0
2006	0.03	0.06	1231	1505	1.00	131	0
2007	0.05	0.07	1449	1519	1.00	170	0
2008	0.04	0.04	2030	2063	1.00	166	0
2009	0.05	0.05	2710	2994	0.94	271	15
2010	0.10	0.05	3702	2912	1.00	539	0
2011	0.09	0.04	3280	1594	0.95	359	18
				Sum		3849	222
				Mean	0.95	226	13
				SD	0.09	148	22
Indian Ocean							
1995	0.12	0.04	2275	2247	0.79	379	79
1996			1998	1953			
1997			2247	1364			
1998	0.05	0.01	1998	1332	0.86	106	15
1999			1617	1622			
2000			5076	3669			
2001			4281	4278			
2002			5103	3107			
2003	0.06	0.02	3883	4136	0.60	284	113
2004	0.06	0.00	3449	4927	1.00	190	0
2005	0.03	0.01	4443	5635	0.67	190	63
2006	0.07	0.00	5295	5635	0.86	376	54
2007	0.10	0.01	5114	4676	0.92	563	47
2008	0.04	0.00	4748	4236	1.00	212	0
2009	0.01	0.00	4940	1989	1.00	64	0
2010	0.02	0.01	5267	1725	1.00	124	0
2011	0.01	0.02	5320	2050	0.80	94	19
				Sum		2581	390
				Mean	0.86	235	35
				SD	0.14	153	39

to be carried away towards America, and on the other hand, young marine turtles born on American beaches seem to remain in the northern hemisphere, leading to a low abundance of this stage of life that may interact with purse-seine gear.

It is worthwhile noting that in this study, observer data collection do not include possible turtle interaction and mortality from two sources: (i) turtles entanglement in the deeper part of the net hanging underneath the DFADs (as this cannot be seen by observers when a DFAD is visited but not hauled onboard) and (ii) the ghost fishing problem occurring when floating devices are lost. Pieces of net, hanging underneath the DFAD, are believed to be the cause of some marine turtle mortality by entanglement and subsequent drowning (see review in Hall and Roman, 2013). The cryptic mortality might be particularly serious when the lost DFADs drift closer to nesting locations leading to a significant mortality of marine megafauna (Shanker et al., 2003). However, information on the number of DFADs deployed is still lacking in the Atlantic and Indian oceans (Dagorn et al., 2013), with only some estimates for the Pacific Ocean (9 813 DFADS deployed 2008, WCPFC, 2009). Hall and Roman (2013) estimated that the additional mortality due to lost DFADs in the Pacific Ocean could be in the order of 80–100 marine turtles per year. This should also be assessed in relation to the estimated 6400 000 tons of different fishing gears lost each year (Wilcox et al., 2012). However, it is important to note that European Union purse seiners operating in the Atlantic and Indian oceans recently started using non-entangling DFADs with non-meshed material both in the surface structure and sub-surface component of the DFADs.

4.3. Key conservation lessons from bycatch patterns

In addition to the assessment of the global level interaction between purse-seine fishery and marine turtles in the Atlantic and Indian oceans and the impact of the different fishing modes, other key regional lessons can be drawn from this study in order to understand the spatial pattern and distribution of marine turtle species and life stages. For instance, the bycatch pattern observed for both hawksbill and green turtle is interesting to consider. These two species are mainly coastal species (Marquèz, 1990) which are found in the open sea only during breeding migrations (Limpus et al., 1992; Gaos et al., 2012) with a very specific behaviour which has them travelling fast and not feeding (Luschi et al., 2007;

Benhamou et al., 2011). This has the effect of decreasing the chances of interaction with purse-seine activities. In contrast, juveniles use the pelagic habitats for a long period drifting within the dominant currents (e.g. Hamann et al., 2011; Proietti et al., 2012), which increases their chances of interacting with purse-seine activity. Such behaviour may explain why juveniles of these two species are observed most frequently on purse-seine sets, both in the Atlantic and Indian oceans.

European purse-seine bycatch patterns also reflect the nesting distribution of species. It was noted for instance that interaction with the leatherback turtle in the Indian Ocean is a rare event whereas in the Atlantic Ocean it is one of the turtles most frequently captured by European purse-seiners. Such a result is a reflection of the nesting distribution of this species and its oceanic behaviour in both oceans. In the western Indian Ocean, nesting sites of leatherback are rare and small (Nel et al., 2013) and feeding grounds are located in higher latitudes out of the European purse-seine fishing activity (Luschi et al., 2006). The impact of the European purse-seine activity is thus expected to be limited. In contrast, the interaction results for the Atlantic Ocean are not surprising as there are two large nesting colonies in the eastern part of the Atlantic Ocean, hosting several tens of thousands of leatherback nesting in the Guinea and in the Gabon (see review in Eckert et al., 2012). Interestingly the two main hotspots of interaction with leatherbacks are observed off the coast of those nesting sites. A similar situation occurs with the olive Ridley in the Indian Ocean where increased interactions occur in the northern part of the European purse-seine fishing area (Fig. 4). This correlates with nesting activity of this species in the Indian Ocean as the main nesting sites are situated in the northern hemisphere (Shanker et al., 2003) with few records of nesting from the south west Indian Ocean (Frazier, 1975).

Another interesting lesson came from the reporting by observers of *Lepidochelys kempii*. If we compare the normally accepted distribution in the Atlantic Ocean (Wallace et al., 2011), this species is not supposed to be found in the European purse-seine fishing area. It is therefore necessary to note that some turtle data, suggesting Kemp's Ridley turtles were recorded as by-catch, used in this study could be the result from misidentifications with the olive Ridley turtle as these two species are very difficult to differentiate. It is not suggested that all identifications are definitively wrong and this may be an opportunity to review the global distribution of the Kemp's turtle in the Atlantic Ocean using DNA samples of *Lepidochelys* sp. accidentally captured in this fishery.

It is suggested that the work done by observers on board purse-seiners, to monitor bycatch and improve our understanding of the interaction between this fishing activity and megafauna, would be highly advantageous to enhance large scale onboard observers programs by collecting tissue samples and associated biological parameters from vulnerable and migratory species such as marine turtles. Such a collection opens the door to solving key issues regarding species at sea distribution and the behaviour of turtles at all life stages. In the case of marine turtles, information provided by genetic sampling could contribute to a better understanding of the distribution of all stages of life based on their origin, *i.e.* identified Management Units or rookeries. Filling in this key gap could be a key advance in helping to mitigate the impact of bycatch by other fisheries.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.06.020.

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CHAPITRE 3 – SYNTHESE : EVALUER LES INTERACTIONS AVEC LA PECHE

La pêche est reconnue pour avoir un impact important sur la mégafaune marine (Lewison et al., 2014) et tout particulièrement sur les tortues marines dans tous les océans (Wallace et al., 2010b). Les travaux de Bourjea et al. (2008; 2014; Chapitre 3, section 1,2), associés à ceux de Petersen et al. (2009) et Humber et al. (2011) sont des références clés aujourd'hui pour avoir une bonne vision des niveaux d'interactions s'opérant entre la pêche, qu'elle soit industrielle ou artisanale, et les tortues marines dans l'océan Indien occidental. Ces travaux ont contribué à fournir une évaluation, quantitative ou qualitative, de ces interactions en fonction de zones géographiques définies. Ils ont permis d'identifier d'une part les principales menaces qui pèsent sur ces espèces, et d'autre part de lever le voile sur le niveau d'interactions réel de certaines activités que l'on soupçonnait de fortement les impacter (Bourjea et al., 2014).

D'un côté, il y a la pêcherie industrielle et semi-industrielle, composée dans l'océan Indien d'unités dont la taille varie en général entre 12 et 100 mètres, exploitant un engin de pêche défini et ayant une capacité très importante à prospecter des zones géographiques éloignées de leur base. Dans le sud-ouest de l'océan Indien, on retrouve 3 grandes pêcheries, la pêche au chalut ciblant les crevettes, la pêche à la palangre dérivante horizontale ciblant les thons tropicaux ou l'espadon (*Xiphias gladius*), et la pêche thonière océanique à la senne tournante ciblant les thons tropicaux.

La pêche au chalut à crevettes, réputée pour interagir très fortement avec les tortues marines qui peuvent partager les mêmes habitats côtiers que les crevettes, est une activité dans l'océan Indien occidental (1) en perte de vitesse, essentiellement à cause de contraintes économiques et de disponibilités de la ressource, (2) très fortement règlementée et (3) associée à des mesures d'atténuation obligatoire de l'impact de cette activité sur les tortues marines (voir pour plus de détails Fennessy, 2012). Les outils mis en place pour atténuer ces captures accidentelles sont aujourd'hui techniquement maîtrisés et ont démontré leur effet très positifs (les Turtle Excluding Device – TED ou plus généralement les By-catch Excluding Devices – BED). Il faut noter cependant que, même si la pêche au chalut de fond est aujourd'hui beaucoup moins active que par le passé sur les côtes d'Afrique de l'Est et Malgache, très peu de statistiques de pêche fiables sont disponibles, ou pour le moins accessibles, et un certain flou persiste sur l'impact réel de cette activité sur les ressources non ciblées. Par mesure de précaution, il semble donc prioritaire à l'avenir d'avoir une meilleure vision de cette activité à Madagascar et en Afrique de l'Est afin de mieux en évaluer l'impact sur la mégafaune marine. La mise en place récente de la Commission des Pêches du Sud-Ouest de l'Océan Indien (SWIOF-C), un organe consultatif de gestion régionale des pêches ayant pour objectif général la promotion de l'exploitation durable des ressources marines de cette région, pourrait à l'avenir jouer un rôle primordial de suivi de cette activité.

Les activités de pêche à la palangre dérivante et à la senne océanique sont actuellement bien mieux connues. Bourjea et al. (2014) ont mis en évidence que la pêche à la senne océanique a un impact direct extrêmement faible sur les tortues marines, et de manière générale sur la mégafaune. Ces auteurs ont conclu que l'impact de cette activité sur les espèces menacées était

négligeable par rapport aux autres activités de pêche présentes dans la région (voir ci-dessous), du moins concernant les captures, autour des DCP en particulier.

La palangre dérivante est une activité de pêche connue dans tous les océans pour interagir fortement avec ces espèces, avec par exemple un nombre estimé de 200 000 tortues caouannes capturées accidentellement par cette pêcherie dans le monde en 2000 (Lewison et al., 2004). La gestion de ces interactions est malheureusement très difficile car le niveau d'interaction avec les tortues marines est très fortement dépendant de la stratégie de pêche (espèce cible, caractéristiques de l'engin, type d'appât, saison, zone) qui est différente en fonction de la flottille de chaque pays, mais aussi variable au sein de chaque flottille et de chaque navire en fonction de la période de l'année. La mise en place de mesures d'atténuation obligatoires et généralisées comme par exemple l'utilisation d'hameçon circulaire (Read, 2007) semble donc difficile pour l'instant et pourrait n'avoir aucun impact sur les populations de tortues marines tout en contraignant et pénalisant inutilement certaines flottilles. Une gestion au cas par cas, essentiellement basée sur une approche spatio-temporelle semblerait être la solution plus efficace pour optimiser le ratio « efficacité de la mesure / contraintes économiques de mise en place ».

Dans tous les cas de figure, la pêche à la senne et la pêche à la palangre dérivante sont actuellement très bien suivies et gérées par la Commission des Thons de l'Océan Indien (CTOI), un organisme régional de gestion des pêches. Un groupe de travail dédié aux captures accidentelles (Groupe de Travail sur les captures accidentelles et les Ecosystèmes) a été mis en place depuis 2005. L'une des principales conclusions de ce groupe pour la mégafaune marine est le manque de données disponibles pour l'élaboration d'évaluations fiables de l'impact des pêcheries sous gestion CTOI (IOTC-WPEB09, 2013). Ces réflexions ont cependant permis d'élaborer un certain nombre de résolutions et de recommandations permettant de mieux évaluer les niveaux d'interactions et de les limiter. L'une des recommandations pour hiérarchiser les menaces qui pèsent sur des espèces capturées accidentellement a été la mise en place d'approches de type Evaluation des Risques Ecologiques (Ecological Risk Assessment – ERA). Cependant, du fait de la pauvreté en données disponibles par engin, des faibles niveaux de captures accidentelles recensés et des traits de vie complexes des tortues marines, la mise en place d'ERA quantitatif reste très difficile. L'option choisie par la CTOI a été de lancer un ERA semi-quantitatif sur les interactions tortues marines / pêcheries sous gestion de la CTOI associé à une approche de productivité - sensibilité (productivity – susceptibility Analysis – PSA; Nel et al., 2013). Les conclusions ont cependant mis en évidence ce qui était déjà connu, à savoir des niveaux d'interaction décroissants en fonction du type de pêcherie allant de la pêche au filet industriel (engin non utilisé dans le sud-ouest de l'océan Indien) à la pêche à la senne, en passant par la palangre dérivante. Mais les auteurs ont souligné que les résultats de cette approche restent très incertains. Ils ont clairement démontré la nécessité d'acquérir des données quantitatives sur ces interactions pour les fiabiliser et pouvoir fournir aux gestionnaires des propositions concrètes de gestion de ces ressources fragiles.

D'un autre côté, on retrouve dans l'océan Indien occidental une pêcherie artisanale côtière, largement dominante comme dans le reste du monde (>95%; Pauly, 2006) et qui est très

souvent vivrière et opportuniste, la majeure partie des captures étant consommée. Cette pêcherie est composée d'une grande variété d'engins, dont l'effort est difficilement estimable et pour laquelle les statistiques de pêche restent le plus souvent insuffisamment fiables, incomplètes voire inexistantes pour certains pays. Or, il est maintenant reconnu que la pêcherie artisanale est très probablement celle qui impacte, directement ou indirectement, le plus la mégafaune marine dans cette région du monde et notamment les tortues marines (voir synthèse dans Bourjea et al., 2008). Par exemple à Madagascar, il a été estimé que par le passé, entre 11 000 et 15 000 tortues marines étaient capturées par la pêche et lors de la ponte (Rakotonirina et Cooke, 1994). Une étude plus récente a mis en évidence que dans la province de Tuléar uniquement (sud-ouest de Madagascar), les captures de tortues marines étaient de l'ordre de 10 000 à 16 000 individus par an, dont 93% de tortues vertes (Humber et al., 2011), probablement l'espèce la plus impactée par les communautés locales de la région.

Comment justifier ce constat? D'une part parce beaucoup de pays de cette région (e.g. Madagascar, Comores) mangent traditionnellement de la tortue marine (Lilette, 2007). D'autre part, parce que l'espèce de tortue marine dominante dans le sud-ouest de l'océan Indien est la tortue verte exploitant des habitats d'alimentation côtiers et peu profonds (Bjorndal, 1997). Enfin parce qu'il a été démontré récemment que non seulement les tortues vertes exploitent essentiellement des habitats d'alimentation situés le long des côtes est africaines et malgaches, mais aussi que lors de leurs migrations post reproductives, elles migrent en grand nombre autant en milieu océanique que le long de ces côtes, optimisant les risques d'interaction avec toute activité de pêche présente (Bourjea et al., 2013; Dalleau, 2013). Si les études de suivi par satellite récentes ont permis d'identifier des zones prioritaires de gestion de ces interactions avec la pêche artisanale (e.g. le Nord du Mozambique, le nord-ouest Malgache), il n'en reste pas moins que très peu d'informations sont disponibles sur les stratégies de pêche artisanale dans ces zones (quels engins, à quelles périodes, en quel nombre ?) et les niveaux d'interaction qui en découlent, limitant les propositions de solutions pour atténuer leurs impacts.

L'une des solutions possibles pour évaluer ces niveaux d'interaction à l'échelle des engins et permettant d'acquérir des données fiables pour prioriser des actions de limitation des interactions avec ces espèces, est la mise en place d'une approche de type Evaluation Rapide des Captures Accidentelles (Rapid Bycatch Assessment – RBA; Moore et al., 2010). Cette approche, basée sur des enquêtes structurées et ciblées auprès des pêcheurs artisanaux permet de mettre en évidence rapidement par une analyse PSA quels engins impactent quelles espèces et quand. Cette approche a été tentée dans le cadre d'un projet Régional (SWIOFP – South West Indian Ocean Fishery Project) dans 4 pays de la région (Mozambique, Kenya, Tanzanie et Maurice). Cette étude, qui reste cependant une étude pilote non publiée, a confirmé l'intérêt de l'approche et mis en évidence par exemple que la senne de plage traditionnelle est l'engin qui impacte le plus la tortue caouanne au Mozambique (Kiska, 2012).

La mise en place à grande échelle de l'approche RBA, associée aux résultats présentés dans les chapitre 1, 2 et 3 de ce manuscrit et à la dynamique spatiale des tortues marines dans le sud-ouest de l'océan Indien (Dalleau 2013, Bourjea et al., 2013) sont les éléments clés pour déterminer les zones et mesures prioritaires à cibler à l'échelle locale pour limiter les prises

accidentelles. Profitant de la prise de conscience récente des communautés locales des pays du sud-ouest de l'océan Indien pour gérer eux-mêmes leurs Aires Marines Protégées (Rocliffe et al., 2014), un travail d'éducation et de sensibilisation des pêcheurs sur des sites stratégiquement identifiés de chaque pays de la région permettrait de diminuer significativement l'impact de cette activité artisanale sur la mégafaune marine.

CONCLUSION – Recherche et gestion de la mégafaune dans l'océan Indien occidental

LES AVANCEES MAJEURES DE LA RECHERCHE SUR LES TORTUES MARINES

Le travail présenté ici a développé différentes approches scientifiques permettant d'avoir une vision régionale la plus fiable possible de l'état de conservation de la tortue verte dans l'océan Indien occidental. Le travail synthétique de chacune de ces thématiques (évaluation des populations, structure génétique et interaction régionale avec la pêche) fournit, à partir de bases scientifiques concrètes, un état des lieux régional précis sur l'état de santé des populations de cette espèce et sur les priorités de gestion. Ce travail a également permis des avancées majeures dans la compréhension des liens pouvant exister entre les différentes populations dans l'espace et dans le temps, ainsi que de mieux comprendre les menaces auxquelles sont confrontées non seulement la tortue verte, mais également aussi les autres espèces de tortues marines.

La première grande conclusion de ce travail a été incontestablement l'identification de trois unités de gestion génétiques distinctes pour les tortues vertes femelles se reproduisant dans l'océan Indien occidental (Chapitre 2; Fig.4.1). De manière intéressante, les caractéristiques des sites de ponte de ces trois unités sont très différentes (Chapitre 1; Fig.4.1), impliquant de ce fait des conséquences variées. L'unité du nord du canal du Mozambique – NCM, composée d'un grand nombre de sites pontes, très abondants en terme de nombre de femelles et très fortement connectés les uns aux autres, est ce que l'on pourrait considérer le cœur de l'océan Indien. Dans le nord-est, l'unité des Seychelles – SEY est composée d'un grand nombre de sites de ponte mais comprend peu de reproducteurs. Si la faible abondance est compensée par le grand nombre de sites de ponte, cette unité reste potentiellement sensible à une érosion de la diversité génétique. Enfin dans le sud, l'unité du sud du canal du Mozambique – SMC est composée essentiellement d'un unique site de ponte, mais probablement l'un des plus importants au monde, Europa. Si le stock de reproducteurs est très imposant pour cette unité, celle-ci reste dépendante d'un unique site et de toutes les menaces potentielles qu'il subit ou pourrait subir. Il est intéressant de noter ici qu'un lien récent entre les tortues d'Europa et celles de l'Atlantique a été mis en évidence (Chapitre 2, Section 1). Cette connexion est un atout fondamental en terme de conservation car elle permet d'assurer une diversité génétique conséquente dans cette unité et primordiale pour assurer sa capacité à évoluer et à s'adapter, notamment dans le contexte actuel de changement climatique rapide.

L'UICN utilise actuellement des unités de gestion régionales (Régional Management Unit – RMU) des tortues vertes dans l'océan Indien (Wallace et al., 2011) pour la détermination par région de son statut UICN. Dans le cadre de cette approche, le sud-ouest de l'océan Indien représente une seule unité régionale (Fig.4.2). Les résultats acquis dans le cadre des chapitres 1 et 2 ont permis d'apporter de mieux évaluer les abondances de populations en reproduction et d'affiner la structure génétique de cette espèce dans le sud-ouest de l'océan Indien. Ces résultats

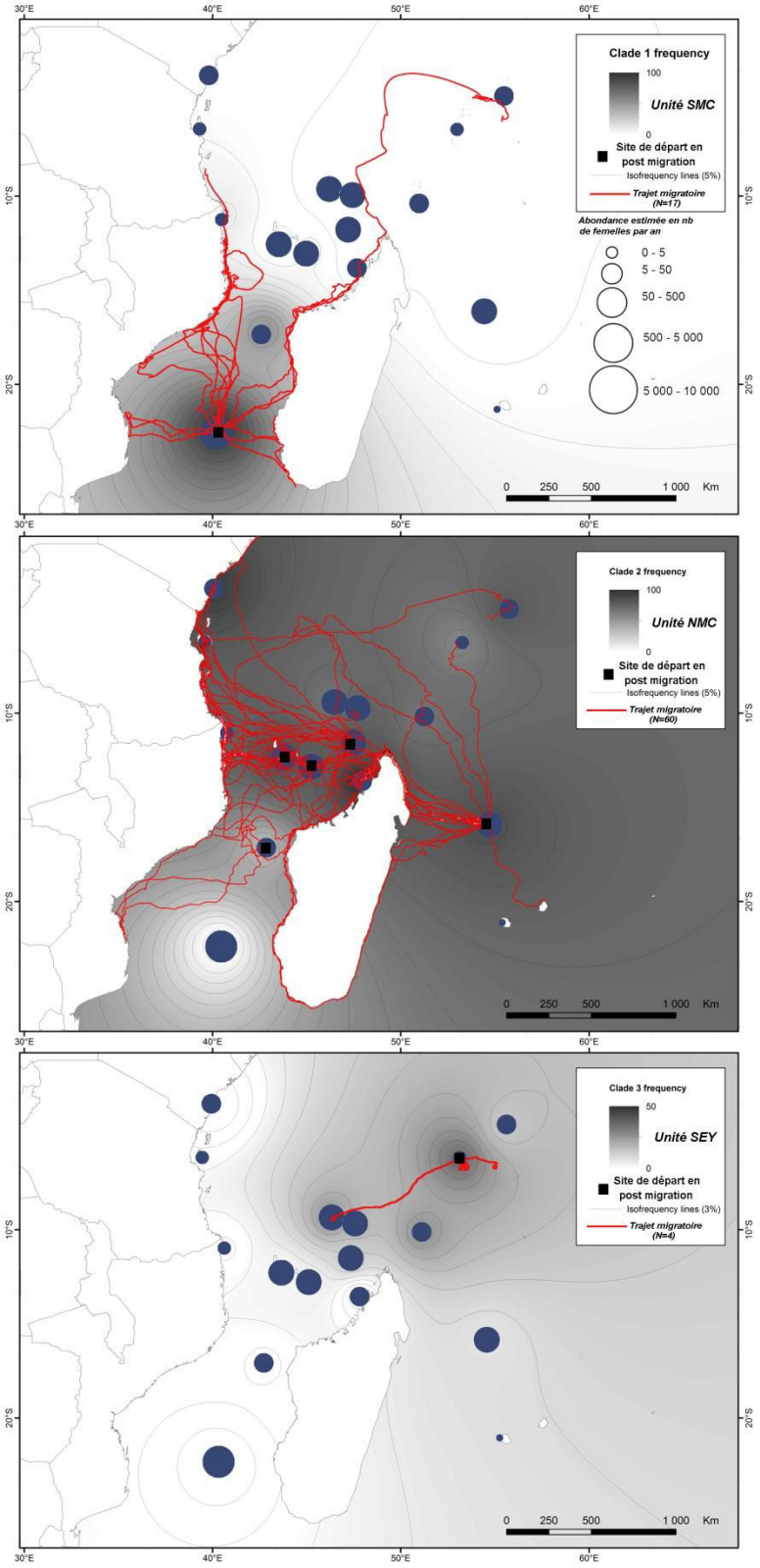

Fig.4.1 : Couplage de la modélisation de la structure génétique (Chapitre 2, Section 2), de l'abondance de femelles de tortues vertes en reproduction (Chapitre 1) et des trajectoires post reproduction (Bourjea et al., 2013) de la tortue verte se reproduisant dans les principaux site de ponte du SOOI. SMC = Unité Sud du Canal du Mozambique ; NMC = Unité Nord du Canal du Mozambique ; SEY= Unité des Seychelles. Les cercles bleus indiquent les abondances estimées du nombre de femelles de tortues vertes se reproduisant. Les traits rouges indiquent les trajectoires post reproduction des tortues vertes.

pourraient permettre d'affiner le dessin actuel de cette unité de gestion régionale UICN mais nécessiteraient des données complémentaires sur les migrations, les sites finaux d'alimentation ou encore les caractéristiques de la dispersion océanique des juvéniles étaient disponibles. Les données de génétiques ont commencé à être couplées aux données de télémétrie satellitaire pour renforcer l'hypothèse d'un stock séparé au niveau des Seychelles (Chapitre 2, Section 2; Fig.4.1 - SEY). Les résultats semblent confirmer que SEY est une unité indépendante des deux autres. Une très récente étude sur les trajets migratoires post reproductifs des tortues vertes se reproduisant au Chagos (est des Seychelles) montre qu'elles se nourrissent en majorité dans l'archipel Seychellois (Hays et al., 2014). Ce résultat renforce l'hypothèse de départ sur l'unité SEY et pose la question de l'appartenance ou non des Chagos à cette unité. Si l'on rajoute les données satellitaires actuellement disponibles dans cette région (Bourjea et al., 2013; Dalleau, 2013), on constate que pour les unités SCM et SEY, à quelques rares exceptions près, la distribution spatiale des femelles depuis les sites de reproduction vers leur site d'alimentation tend à rester dans l'unité (Fig.4.1 – SEY et SMC). Cependant, lorsqu'on regarde les trajets post-reproduction des femelles depuis les sites de ponte de l'unité NMC, on remarque qu'ils tendent à se connecter avec les deux autres unités (Fig.4.1 – NMC). C'est en effet le constat de l'analyse fine des résultats de ce suivi par satellite qui a démontré un mélange sur les aires d'alimentation des tortues vertes femelles se reproduisant dans les sites des trois unités de gestion génétique (Fig.4.3; Bourjea et al. 2013; Dalleau, 2013).

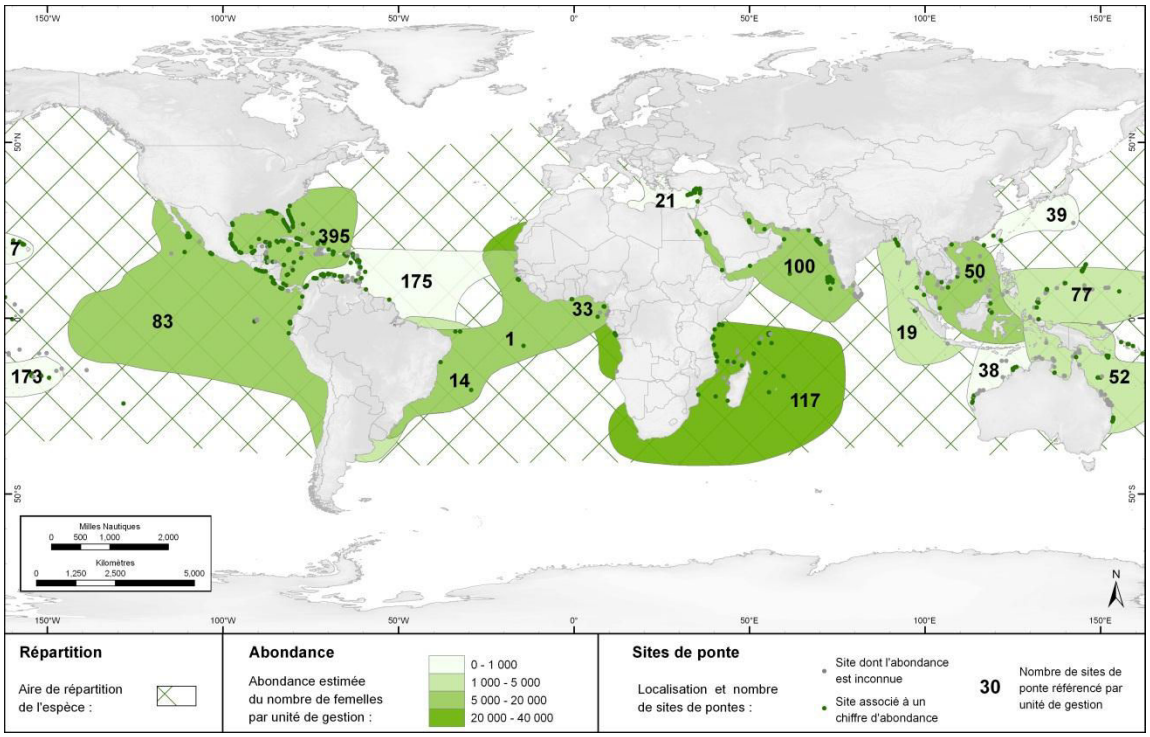

Fig.4.2 : Synthèse des connaissances sur la tortue verte dans le monde : site de ponte, abondance et unités de gestion. Modifié d'après Wallace et al. (2011).

Sur la seule base de ces éléments, il semble donc difficile de déterminer définitivement si ces trois unités de gestion génétique constituent ou non des unités de gestion globales et indépendantes de tortues vertes. Cette première approche pour mieux structurer les

populations au niveau régional a permis cependant de mieux cerner les menaces qui pèsent sur ces unités de gestion, à savoir la dégradation des habitats, le prélèvement illégal des adultes, des immatures et des œufs, et la pêche (Chapitre 3, Section 1).

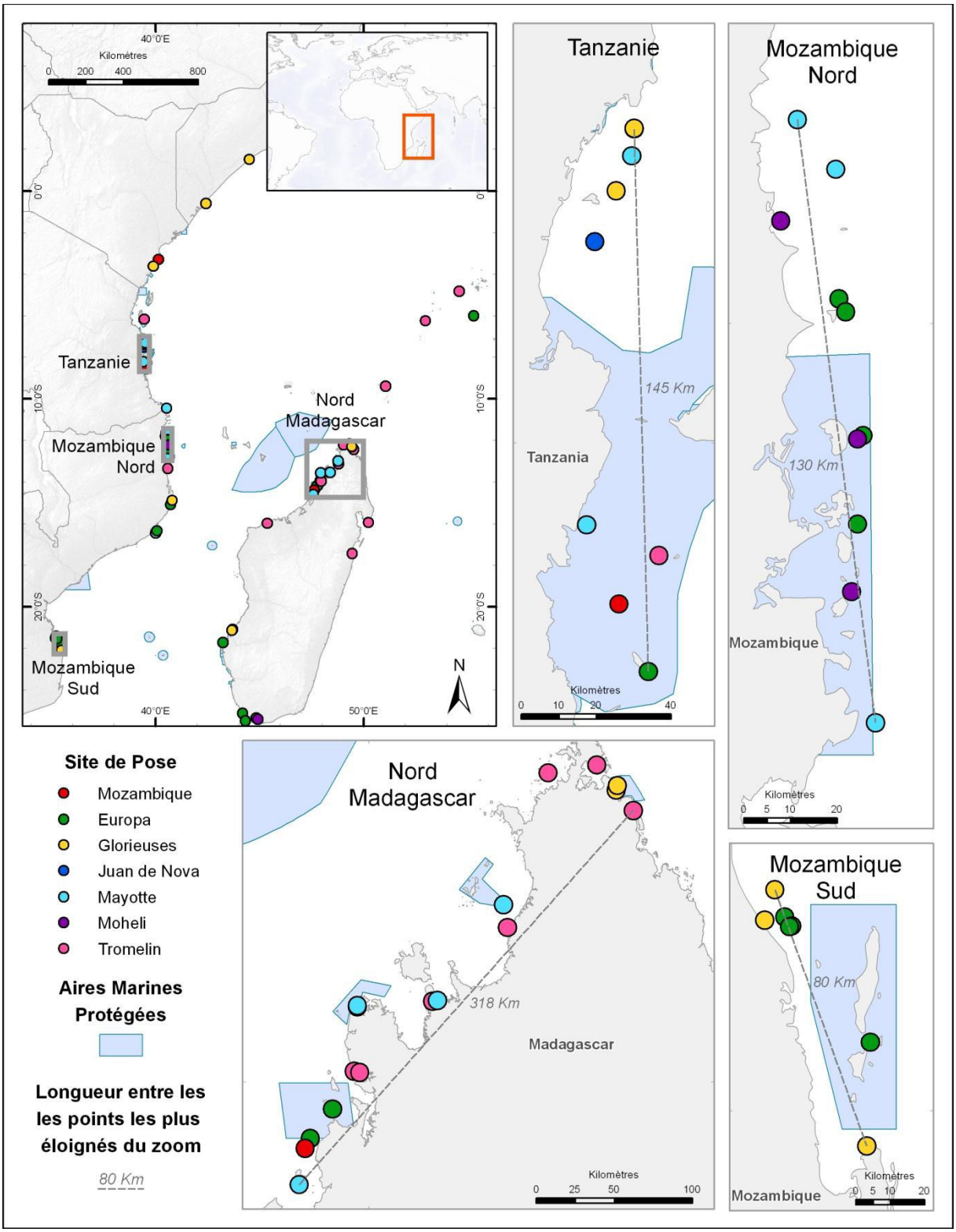

Fig.4.3 : Distribution régionale des tortues vertes femelles sur les aires d'alimentation du sud-ouest de l'océan Indien en fonction du site de reproduction d'origine (« Site de Pose »). D'après Bourjea et al., 2013)

La seconde grande conclusion de ce travail de thèse a été de mettre en évidence qu'en termes d'interactions avec les activités de pêche, la menace principale qui pèse sur les tortues marines dans le sud-ouest de l'océan Indien n'était pas la pêche industrielle, même si celle-ci a probablement un impact non négligeable, mais la pêche artisanale côtière de subsistance (Chapitre 3, Section 2). En effet, si d'un côté la pêche à la senne océanique européenne, qui a capturé plus de 350 000 tonnes de thons en 2012, ne tue accidentellement que quelques dizaines de tortues marines par an, la pêche artisanale côtière des pays riverains de la région au contraire est probablement responsable tous les ans de la mort de plusieurs dizaines de milliers d'individus de ces espèces (Chapitre 3, Section 2). L'association de ces niveaux d'interaction par engin à un modèle d'estimation de la densité de dispersion entre site de ponte et aire d'alimentation des tortues vertes femelles (Bourjea et al., 2013) permet de mettre en évidence des hotspots d'interactions potentiels entre cette espèce et la pêche artisanale : le nord du canal du Mozambique et la côte ouest malgache et (Fig.4.4).

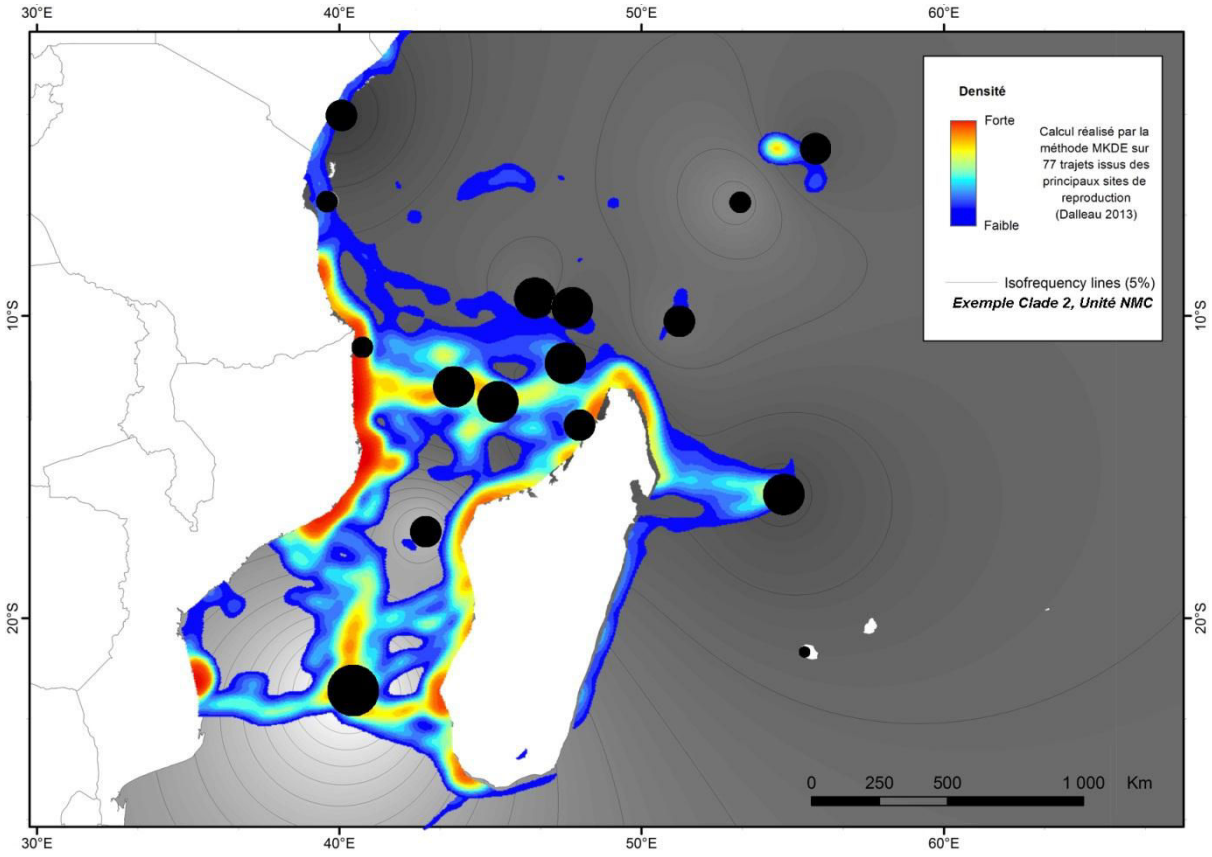

Fig.4.4 : Représentation spatiale conjointe de la modélisation de la structure génétique (Chapitre 2, Section 2, exemple Clade 2 - NMC), de l'abondance de femelles en reproduction (Chapitre 1) et de l'estimation de la densité de dispersion des femelles en migration post-reproductive (Bourjea et al., 2013)

Priorités de la recherche sur les tortues marines

Les principales conclusions de ce travail sur les tortues vertes soulèvent donc une question essentielle, celle de l'identification de nouvelles unités de gestion régionales de la tortue verte dans le sud-ouest de l'océan Indien. L'unité définie actuellement (Fig.4.2) peut-elle ou doit-elle être affinée ? Pour répondre à cette question il faudrait savoir comment se distribue et se structure l'ensemble de la ou des populations de tortues vertes (adultes et juvéniles) dans la région.

L'un des aspects les plus importants pour mieux comprendre la structure globale des populations de tortues vertes dans la région est de déterminer l'origine des tortues adultes sur les habitats d'alimentation. L'approche par télémétrie satellitaire semble indiquer que les populations des trois unités génétiques se mélangent sur les sites d'alimentation (Bourjea et al., 2013; Dalleau, 2013). Mais du fait du faible échantillonnage (n= 77), ces données ne sont pas suffisantes pour tirer des conclusions définitives. Entre autres, il faudrait compléter ces suivis satellitaires au niveau des Seychelles, en augmentant l'échantillonnage au niveau du groupe des Amirantes, mais aussi en rajoutant les sites des îles Granitiques (Mahé, North, Bird) et Coralliennes (Aldabra et Cosmoledo). L'approche par la génétique des populations a déjà fait ses preuves en la matière (e.g. la tortue verte dans l'Atlantique nord, Lahanas et al., 1998) et notamment les analyses de stocks mixtes (Mixed Stock Analyses; Manel et al., 2005; Pella et Masuda, 2005), ou encore les analyses de stocks mixtes multiples (Bolker et al., 2007). Elle serait sans conteste la meilleure solution pour comprendre la structuration des populations de tortues vertes sur les sites d'alimentation dans cette région du monde. La difficulté, non négligeable dans le cas présent, est la capacité des équipes de recherche à mettre en place un échantillonnage sur des adultes (>150 kg) seulement accessibles sous l'eau (3m<profondeur<30m).

Un autre aspect indispensable pour définir ces unités de gestion régionales est la compréhension de la dispersion spatio-temporelle des juvéniles aux différents stades. Le même type d'approche que celui de la génétique pourrait être développé dans ce cas. En effet, elle a déjà permis par exemple dans le cas de la tortue caouanne, de mettre en évidence que les stades pélagiques capturés accidentellement dans l'Atlantique sud proviennent effectivement de l'Atlantique pour partie, mais également de l'océan Indien occidental (Shambling et al., 2014). Dans le cas de ces stades, l'approche par télémétrie satellitaire semble être également un outil indispensable pour comprendre la dynamique spatiale. A l'image des découvertes récentes sur le comportement migratoire des premiers stades de vie des tortues caouannes dans l'Atlantique nord (Mansfield et al., 2014), l'utilisation de balises miniatures sur de très jeunes tortues vertes pourrait contribuer à comprendre cette dispersion océanique et le mélange entre populations qui en découle. Enfin, l'utilisation de balises de type FAST LOC GPS (acquisition GPS et transmission de l'information au satellite par la technologie Argos) pourrait aussi permettre de mieux comprendre les temps de résidence et les changements au niveau régional d'habitats de développement, déjà observés pour ces stades au Brésil (Naro-Maciel et al., 2007). De la même manière que pour les adultes sur leur habitat d'alimentation, la difficulté reposera sur la capacité

des chercheurs à capturer ces stades à la côte, mais surtout lorsqu'ils sont en pleine mer. L'une des solutions pour accéder à ces stades océaniques serait alors de travailler avec des observateurs embarqués (Voir Chapitre 3, Section 3 et plus loin).

Enfin, il est important de noter qu'une série de priorités de recherche sur d'autres thématiques (biologie de la reproduction, impact du changement climatique…) élargie à toutes les espèces de tortues marines présentes dans l'océan Indien, a été rédigée dans le cadre du plan national d'actions en faveur des tortues marines des territoires français de l'océan Indien 2015-2020 – PNA pour La Réunion, Mayotte et les Eparses, mais aussi au niveau régional (Philippe et al. soumis).

Les approches à favoriser pour la mégafaune marine

Au-delà de la problématique «tortue marine», l'acquisition de données pertinentes et le développement de méthodes scientifiques qui répondent aux besoins de la conservation de la mégafaune sont difficiles (voir introduction). Différentes options sont cependant à prendre en considération à l'avenir.

Favoriser le développement d'observateurs « scientifiques » embarqués.

Un des points clés relevé tout le long de ce travail est de comprendre les mouvements des tortues marines et notamment lorsqu'elles sont en pleine mer (migration vers les sites de reproduction, phases pélagiques juvéniles – « the lost years »). Très peu d'informations sont disponibles sur ces stades essentiellement à cause de la difficulté à accéder aux individus. Dans un contexte global d'augmentation des programmes observateurs pour répondre aux obligations européennes et à celle des organismes régionaux de gestion des pêches (e.g. 5% de couverture de l'activité de pêche totale de chaque pays, résolution CTOI 11/04, article 4), il semble primordial que la recherche s'adosse à ce développement en donnant les moyens à ce réseau d'évoluer vers un système d'observateurs scientifiques embarqués. Ces derniers auraient toujours comme priorité le suivi de l'activité de pêche, mais pourraient dédier une partie de leur temps à des échantillonnages spécifiques sur des programmes estimés prioritaires. La faisabilité de cette évolution tiendrait d'une part à la capacité de la recherche à former ces observateurs, et d'autre part aux coûts qu'elle engendrerait. Car si un observateur a une partie de son temps dédié à de l'échantillonnage pour la recherche, il sera nécessaire d'augmenter le nombre d'observateurs pour assurer le bon suivi des statistiques de pêche. Ponctuellement, cette approche scientifique de l'observateur est déjà opérationnelle, mais reste à un niveau national et d'une pêcherie (exemple : l'observatoire thonier de l'IRD et ses observateurs). Pour être les plus efficaces possible et couvrir l'ensemble des zones d'un océan, ces programmes nationaux doivent se mettre en réseau afin d'assurer un accès le plus large possible aux zones océaniques. Un certain nombre d'initiatives régionales se sont récemment développées en ce sens dans le sud-ouest de l'océan Indien (e.g. le projet SWIOFP, www.swiofp.org), laissant espérer dans un avenir proche une structuration régionale des observateurs embarqués. Reste à espérer que cette réflexion inclut cet aspect scientifique qui permettrait sans aucun doute d'améliorer la recherche sur les espèces pélagiques. A l'image de l'identification de l'origine des tortues caouannes capturées accidentellement dans l'atlantique sud possible (Shambling et al., 2014),

cette approche permettra de mieux comprendre les mécanismes de dispersion de beaucoup de grands vertébrés marins et de lever des verrous clés de la gestion de ces espèces.

Renforcer les études sur la compréhension de la connectivité des espèces et des processus qui les dirigent.

La connectivité en milieu marin correspond à l'échange d'individus entre aires géographiques distinctes, qu'il soit physique (mouvement de l'individu) ou génétique (flux de gènes par la reproduction). L'un des moyens les plus efficaces d'estimer cette connectivité est d'utiliser une approche de génétique des populations (voir Chapitre 2). Améliorer les connaissances sur les schémas de connectivité au niveau régional nécessite une approche non pas mono-spécifique (Chapitre 2), ni mono-groupe spécifique (e.g. des espèces de poissons), mais multi-groupes d'espèces marines (e.g. des espèces de poissons, de crustacés, d'éponges, d'algues…etc). L'intégration dans les modèles de génétique des populations de plusieurs espèces vivant dans la même zone est en effet un enjeu majeur à l'avenir si l'on veut mieux discerner les effets «espèce dépendant» des effets «environnement dépendant» influençant la connectivité des organismes marins dans cette région. Dans le contexte de la protection de la biodiversité, une telle connaissance est indispensable pour replacer dans un contexte régional des actions qui sont menées localement, et surtout pour positionner au mieux les différentes zones de protection les unes par rapport aux autres afin d'en maximiser les effets bénéfiques. Une application intéressante de la génétique des populations comme outil d'aide à la gestion est la comparaison des modèles de connectivité de 27 espèces marines de différents groupes zoologiques de l'archipel hawaïen (Toonen et al., 2011). Cette approche a abouti à la conclusion que, pour une gestion efficace de la biodiversité marine dans cet archipel, il était nécessaire de mettre en place au moins cinq unités de gestion distinctes dans l'espace géré.

Développer les approches intégrées

Le pari de la recherche d'aujourd'hui est de développer des outils capables d'incorporer des méthodologies qualitatives et quantitatives pour explorer l'écologie à la fois d'une espèce et de communautés d'espèces partageant le même habitat pour fournir au gestionnaire les limites spatiales optimales du système à protéger. Le problème principal de ces approches réside dans la qualité des données et leur regroupement, sachant qu'en général elles sont très hétérogènes (méthodes d'échantillonnages, efforts, nombre, échelles temporelles, échelles spatiales; e.g. Pais et al., 2012). Les avancées récentes en modélisation statistique (entre autre les approches probabilistes Bayesiennes) permettent de résoudre un certain nombre de ces problèmes et peuvent, par exemple, transformer des jeux de données spatialisés complexes, ponctuels et hétérogènes en probabilité spatiale de présence, notamment sur des zones ou aucune observation n'a été faite; cette transformation se fait par une extrapolation des données environnantes (Franklin, 2009). De manière plus poussée, et afin de gérer de grandes quantités de données d'origines et de formes différentes, des approches comme la modélisation de l'entropie maximale (Maximum Entropy modelling) deviennent de plus en plus des outils de la conservation et de la gestion du milieu marin (e.g chez le dauphin à long bec : Thorne et al., 2012; chez les oiseaux marins : Arcos et al., 2012). Cette approche, cherchant la distribution théorique du jeu de données ayant la plus grande entropie (contenant le plus grand nombre

d'informations réelles) a été développée récemment pour comprendre la distribution de la mégafaune marine (essentiellement des cétacés, des pinnipèdes, des tortues marines et des grands poissons téléostéens) dans la Manche. L'objectif était d'identifier des zones clés pour la conservation de ces espèces dans une des zones présentant un des trafics maritimes les plus importants de la planète (McClellan et al., 2014). Ce type d'approche, couplé aux approches de connectivité, pourrait être envisagé dans l'océan Indien occidental, une zone où les jeux de données spatialisés sur la mégafaune commencent à être considérables (oiseaux marins, tortues marines, cétacés).

DE LA RECHERCHE A LA GESTION : OPTIMISER LA CONSERVATION DE LA MEGAFAUNE

Contribution au Plan National d'Actions sur les tortues marines

La lutte contre la perte de la biodiversité est un engagement fort du gouvernement français et de l'Union Européenne. Cet engagement s'est traduit par la signature par l'Union Européenne et la France de la convention de la diversité biologique lors du sommet de la Terre de Rio de Janeiro en 1992. Parmi les outils développés dans le cadre de la stratégie nationale pour la biodiversité adoptée par la France en 2004, l'État français a souhaité mettre en place des plans de restauration nationaux pour les espèces dont l'état de conservation n'est pas favorable. Le Grenelle de l'environnement (2012) et plus précisément le programme visant à «stopper la perte de la biodiversité» a conclu à la mise en œuvre des plans de conservation et de restauration dans les 5 ans pour les 131 espèces présentes sur le territoire français (métropole et outre-mer) et considérées comme en danger critique d'extinction sur la liste rouge mondiale de l'UICN. Ces plans visent entre autre à organiser un suivi cohérent des populations de l'espèce ou des espèces concernées et à mettre en œuvre des actions coordonnées favorables à la restauration ou au rétablissement de ces espèces ou de leurs habitats.

L'ensemble des résultats présentés dans les chapitres 1, 2 et 3, ainsi que d'autres que j'ai obtenus et qui ne sont pas présentés dans le présent travail, ont été largement utilisés pour l'élaboration du volume 1 (Partie commune : Diagnostic, stratégie opérationnelle et actions régionales) du plan national d'actions en faveur des tortues marines des territoires français de l'océan Indien 2015-2020 – PNA (Philippe et al. soumis) ainsi que pour les trois autres volets dédiés aux trois territoires concernés, à savoir La Réunion, les Eparses et Mayotte. L'élaboration de ce plan, unique du fait qu'il cible 5 espèces de tortues marines et inclut 3 territoires, n'a pu être possible que grâce à la vision régionale décrite tout au long de cette thèse. En effet, l'aspect novateur de ce plan tient dans le fait qu'il comprend un volet régional spécifique, c'est-à-dire qu'il replace les tortues marines de chaque territoire dans le contexte de l'unité de gestion régionale définie pour cette espèce (Wallace et al., 2011; Fig.4.2). Ce PNA a permis de mettre en place une stratégie de conservation à long terme de ces espèces et de planifier les actions prioritaires à mener sur une durée de 5 ans, entre 2015 et 2020 pour chaque territoire et pour l'échelle régionale.

Je ne développerai pas ces actions parfaitement décrites et structurées dans le cadre de ce plan. Par contre, je développerai deux points particuliers non abordés dans le PNA: l'identification de zones prioritaires au niveau régional pour la conservation des tortues marines et le cas des aires marines protégées du sud-ouest de l'océan Indien, pierre angulaire de la protection de la mégafaune marine et peu abordé à l'échelle régionale dans ce plan.

Zones prioritaires de protection

L'ensemble de ce travail, associé aux travaux disponibles sur les tortues vertes et dont les principales conclusions et réflexions ont été présentées tout au long de ce document, permettent de dessiner au niveau régional des zones pour lesquelles il faut être vigilant. Ces zones pourraient avoir un rôle clé dans la préservation des tortues vertes, et plus généralement de la mégafaune marine. Elles sont présentées sur la Fig.4.5. Il me semble important de fournir quelques éléments de synthèse justifiant ces choix.

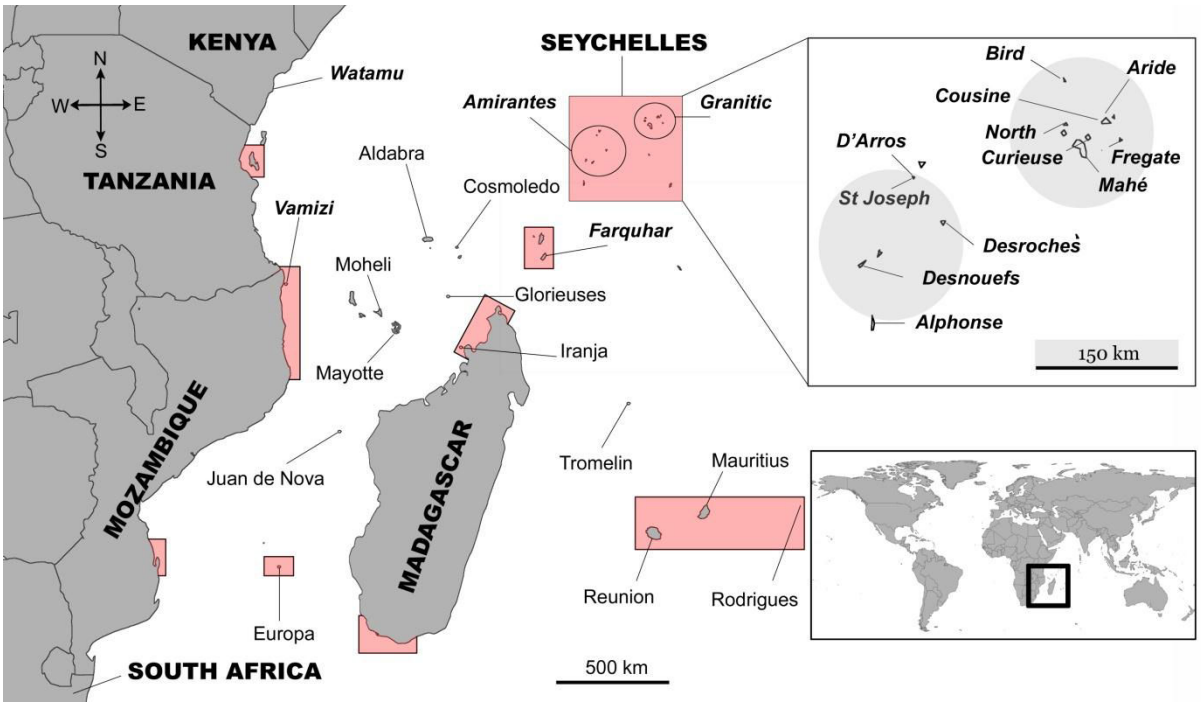

Fig.4.5 : Proposition de zones prioritaires pour la conservation des tortues vertes du sud-ouest de l'océan Indien occidental. Ces zones ont été définies d'après l'analyse réalisée dans ce travail de thèse

Europa, un petit caillou qui porte le nom de tout un continent. De par sa situation géographique dans le sud du canal du Mozambique, l'abondance de ses femelles de tortues vertes, leur diversité génétique spécifique unique dans l'océan Indien et aussi de par la biodiversité en général que cette île héberge, Europa est unique. C'est pourquoi il est indispensable de maintenir les efforts de conservation déployés pour ce site géré par les Terres Australes et Antarctiques Françaises. Ces caractéristiques propres aux tortues vertes, la diversité biologique

de cette île et la gestion actuelle dont elle fait l'objet lui ont entre autres permis d'être désignée comme l'un des quatre sites de référence de l'IOSEA MoU pour les tortues marines dans l'océan Indien. Il convient donc à l'avenir de continuer, voire favoriser, les programmes de recherche sur cette île et de s'assurer de l'application des mesures de conservation.

Les zones des Seychelles, myriades d'îles isolées. De nouveau, les caractéristiques génétiques uniques des tortues marines de cette région, associées à un nombre de reproducteurs faible et distribué sur un grand nombre d'îles différentes, implique une vigilance accrue en terme de conservation. De plus l'isolement de ces îles, le statut d'AMP de quelques-unes d'entre elles et la politique actuelle du gouvernement seychellois très axée sur la conservation de la nature en font des avantages indéniables pour la préservation. Mais ils représentent également un risque potentiel, les surfaces impliquées et les moyens financiers dédiés à l'environnement par les Seychelles pourraient ne pas être suffisants pour assurer une surveillance efficace de ces sites.

Les Mascareignes, sauver les restes du passé. Même si très peu de tortues ont été observées en reproduction sur ces îles (La Réunion, Maurice et Rodrigues) ces 10 dernières années, elles n'en ont pas moins été des sites de reproduction majeurs pour les tortues marines (Ciccione et Bourjea, 2006; 2010). Elles pourraient en outre héberger une population résiduelle de tortues vertes en ponte typique des Mascareignes (Taquet, 2007). Enfin, il a été mis en évidence ces dernières années une augmentation significative du nombre d'immatures en phase de développement sur la côte ouest de La Réunion (Jean et al., 2009), ce qui vraisemblablement pourrait être le cas à Maurice et à Rodrigues. Véritable patrimoine culturel des créoles, il semble donc primordial de considérer ces îles comme des priorités de conservation des tortues marines dans la région.

Le nord du Mozambique, la course au développement. Le nord du Mozambique a été identifié comme une zone clé d'alimentation des tortues vertes se reproduisant dans les îles de l'océan Indien occidental (Bourjea et al., 2013; Fig.4.4). Cette zone est également le centre d'interactions fortes avec les pêcheries artisanales (Chapitre 3). Très récemment, un des plus grands gisements de gaz au monde a été découvert dans la zone des Quirimbas, actuellement en partie sous statut d'aire marine protégée. En considérant que de façon générale, la tendance est à diminuer la taille et les mesures de conservation associées à ces réserves (Mascia et Pailler, 2011; Ritchie et al., 2013), et que la cause est la découverte d'énergies fossiles et la pression économique liée à l'exploitation des ressources (Marvier, 2014), cette zone devrait être considérée pour la décade à venir, comme la zone prioritaire de conservation non seulement des tortues marines, mais de la biodiversité marine en général.

Les zones malgaches, entre subsistance et conservation. Madagascar héberge de nombreux sites de reproduction, même s'ils restent peu importants en terme d'abondance de reproducteurs. En revanche, cette île héberge surtout beaucoup de tortues vertes sur des sites d'alimentation qu'elles fréquentent essentiellement au nord, et au sud (Bourjea et al., 2013; Fig.4.4). Les relations culturelles entre la tortue et les peuples malgaches sont ancestrales (Lilette, 2007) et la consommation de tortues implique des interactions très fortes avec la pêche artisanale (Chapitre 3). Deux zones semblent prioritaires pour la conservation, une au nord, qui comprend déjà un certain nombre d'aires marines protégées, et surtout une au sud où leur absence pourrait être

potentiellement problématique pour ces espèces. Une réflexion doit donc s'engager pour la création d'une ou de plusieurs réserves dans le sud, réflexion qui doit aller au-delà du cas des tortues marines pour définir leur positionnement géographique et leur surface optimale dans un contexte régional. En effet, la création de réserves reste l'outil disponible le plus performant aujourd'hui pour conserver la biodiversité marine et terrestre.

Le cas des Aires Marines Protégées

La protection et la préservation du patrimoine marin sont devenues une obligation pour tous les pays depuis l'adoption de la convention des Nations Unies sur le droit de la mer (article 192; United Nations Convention on the Law of the Sea, 1982). Cette préservation de la biodiversité passe globalement par trois grands types de mesures portées par les gouvernements et les organes internationaux : l'élaboration de réglementations et d'interdictions au niveau national ou international, la conservation *ex situ* et les actions de réintroduction et de renforcement de populations et, probablement la plus importante, la création de parcs et réserves marins dont les statuts juridiques sont très variés et que j'engloberai ici dans le terme général «Aire Marine Protégée» – AMP. L'intérêt de cet outil pour la conservation des ressources marines a été croissant ces 15 dernières années et le sommet mondial pour le développement durable de 2002 a statué sur l'obligation que chaque pays côtier présente au moins 10% d'AMP dans sa zone économique exclusive en 2012 (World Summit on Sustainable Development, 2002), date butoir qui a été prolongée récemment à 2020 (Convention on Biological Diversity, 2010). Aujourd'hui, la surface de l'ensemble des aires marines protégées ne représente que 2% de l'ensemble de la surface des océans (Halpern, 2014). Cette obligation de 10% apparaît judicieuse car les AMP sont l'une des mesures de gestion les plus efficaces pour les tortues vertes en phase néritique. En effet, une analyse mondiale regroupant 116 trajets de tortues vertes en migration post-reproductive dans les trois grands océans a permis de mettre en évidence que 35% des tortues avaient un habitat d'alimentation dans une AMP (Scott et al., 2012). Une étude similaire menée sur 105 tortues vertes suivies par télémétrie satellitaire en parallèle à ce travail de thèse a permis de mettre en évidence que 35% de ces tortues se reproduisant dans les principaux sites de ponte du sud-ouest de l'océan Indien (Chapitre 1) avaient leur habitat d'alimentation dans une AMP (Bourjea et al., 2013). Sachant que les AMP du sud-ouest de l'océan Indien ne représentent que 150 000 km², soit 2,03% de la surface totale (calcul basé sur l'emprise de la Fig. 4.3) et que la présence de tortues marines est un indicateur de la santé des écosystèmes (Jackson, 2001), ce chiffre de 35% est extrêmement encourageant. Il pourrait cependant très probablement être optimisé sur les bases des conclusions du rapport de Bourjea et al. (2013) et des résultats de cette thèse.

Des aires marines protégées dont l'efficacité reste encore à optimiser

Il est cependant primordial dans le cadre d'une réflexion scientifique d'appui à la gestion, de prendre en considération un certain nombre de points techniques en relation avec les AMP.

L'intérêt et l'évaluation de l'efficacité de cet outil de conservation des ressources marines n'est que récent (Boersma et Parrish, 1999; Mangel, 2000) et reste très variable en fonction des zones géographiques ciblées, des pays engagés, des tailles impliquées et des outils associés. J'aborderai ici trois points parmi d'autres qu'il me semble nécessaire de mettre en avant. Le premier est l'évaluation de l'application des règlementations d'une AMP, et malheureusement le constat actuel est qu'il existe beaucoup trop «d' AMP papier» pour lesquelles les limites légales existent bien, mais pour lesquelles les mesures de gestion ne sont pas appliquées (Jameson et al., 2002; Mora et al., 2006). Or l'océan Indien occidental est bordé de pays en voie de développement où la préoccupation première, à juste titre, est la subsistance. Avant d'y développer une nouvelle AMP, il serait judicieux d'évaluer l'efficacité du réseau actuel et de prendre en considération la capacité financière et humaine réelle du pays et du gestionnaire potentiel. Cette approche est trop souvent négligée sous couvert d'afficher un pourcentage élevé de zones marines protégées.

Le second point est le potentiel du sud-ouest de l'océan Indien d'accueil d'AMP qui sont effectivement «efficaces». Une étude récente a mis en évidence que cinq facteurs influençaient le succès en terme de conservation d'une AMP : l'âge (>10 ans), la taille (>100km²), l'isolement, le degré de protection et l'application des mesures de gestion (Edgar et al., 2014). Cette étude a surtout également démontré qu'au-delà de ces cinq facteurs, l'efficacité de l'AMP augmentait proportionnellement au nombre de facteurs impliqués : plus une AMP répond à de critères, plus elle est efficace. Les auteurs concluent que seuls 4,6% de l'ensemble des AMP de la planète remplissent ces 5 conditions. En d'autres termes, une vieille AMP de grande taille, isolée, sous protection intégrale et surveillée de manière efficace représente l'AMP idéale. Si l'on se penche sur la situation du sud-ouest de l'océan Indien, on peut observer que non seulement cette région héberge déjà ce type d'AMP, mais qu'en plus elles sont réparties selon un large gradient latitudinal (les Eparses (voir Chapitre 1) : les îles coralliennes Seychelloises comme Aldabra (patrimoine mondial de l'Unesco), les Chagos (et sa base militaire interdite; Hays et al., 2014), les îles Eparses Françaises (Bourjea et al., 2011). On constate aussi que cette région présente un potentiel pour d'autres sites isolés stratégiquement positionnés comme St Brandon, Agalega, les Amirantes) et qui devraient être considérés comme des sites prioritaires pour les réflexions de mise en place d'AMP.

Sur l'ensemble de ces cinq facteurs, celui qui reste le plus important pour une AMP est l'isolement (Edgar et al., 2014), un facteur qui reste dépendant de la capacité d'un pays à disposer physiquement de sites isolés. Le troisième point que je souhaite aborder est relatif à la notion de réseau. Pour des questions socio-économiques évidentes tout ne peut pas être mis sous statut d'AMP, impliquant une vraie réflexion sur la taille de l'AMP et leur mise en réseau régional. Le constat est que, si des propositions sur des microstructures de protection qui fonctionnent existent (Garcia-Lopez et al., 2014), presque la moitié des AMP de la planète sont approximativement de la taille d'un terrain de football (Wood et al., 2008), et donc faiblement performantes. A l'inverse, de récentes « méga AMP » ont été créées ces dernières années, très probablement dans une optique gouvernementale d'atteindre l'obligation de 10% d'AMP imposée par les Nations Unies. Leur efficacité sur la mégafaune migratrice par exemple peut être remise en question ainsi que la capacité du pays à faire respecter la réglementation sur ces

surfaces irréalistes (Hays et al., 2014). Depuis une dizaine d'années, de nombreuses réflexions ont conclu à l'intérêt de la mise en réseau des AMP d'une région et notamment celui d'intégrer dans ce réseau des AMP intégrales (Wood et al., 2008). Cette réflexion est d'autant plus importante à tenir dans le contexte de la pêche qu'un réseau bien pensé peut être bénéfique à la fois à la biodiversité et aux acteurs de la pêche (Costello et al., 2010). Même s'il est difficile actuellement d'évaluer l'effet réel d'un réseau d'AMP, les avancées de la recherche ont permis de confirmer que cette mise en réseau pouvait, grâce à la connectivité des espèces, compenser les déficiences d'une AMP et notamment celles de petite taille (Gains et al., 2010).

Il nous faut donc pour l'instant continuer de travailler pour accroître nos connaissances sur des modèles biologiques clés et indicateurs de la qualité de l'écosystème dans une optique de meilleure compréhension de la connectivité des ressources marines à l'échelle d'une région océanique. A terme, la mise en commun de ce travail sur l'ensemble de ces espèces pourra permettre de dessiner un réseau régional optimal de structures nationales protégeant notre patrimoine naturel tout en prenant en compte les contraintes socio-économiques auxquelles nous ne pouvons-nous soustraire dans notre société actuelle.

Je terminerai par deux citations.

La première est comorienne. «*Vale vuliyo li dudja de vahano mlango uliyo*», soit littéralement «Là où il a des vagues, se trouve l'issue». En d'autres termes, c'est en faisant face aux problèmes qu'on trouve des solutions. Il ne faut donc pas fermer les yeux sur la dégradation de la biodiversité, il faut l'accepter, la montrer et travailler pour trouver des solutions.

La seconde est plus littéraire. «*Voir le dedans de la mer, c'est voir l'imagination de l'inconnu*», comme le disait Victor Hugo dans Les Travailleurs de la mer. En effet comprendre la mer et mieux la protéger, c'est permettre aux générations futures de continuer à rêver.

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